ARCTIC

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Cover Picture: Midnight sun about June 21 at head of Dease Bay, Great Bear Lake. Note unbroken ice on bay. *Photo: A. E. Porsild*

W. R. B. Battle, Senior Fellow of the McGill University–Arctic Institute Carnegie Program, who was drowned in Baffin Island on July 13.

VOLUME TO BE PUBLISHED ON ARCTIC RESEARCH

R. C. Wallace

The Arctic Institute of North America is concerned with the prosecution of research in the arctic and subarctic regions of the North American continent and in Greenland. The United States, Canada, and Greenland are represented on its Board of Governors. In the eight years during which the Institute has functioned, it has financed, or helped to finance, over one hundred projects of research in these northern areas, in a great variety of fields of scientific endeavour. In so doing, it has assisted in building up a corps of younger scientists competent to work in arctic territory. From these younger men much will be expected in the future. For the need is great.

The Research Committee of the Institute feels that a review of the present status of arctic research in the various fields of science would now be of value both to the scientific worker and to others who are interested in northern development. It was suggested that there would be great value if the present trends and the future needs were emphasized. The Institute has therefore decided to publish a volume of collected papers dealing with the different sciences. The Research Committee has been fortunate in securing the cooperation of highly competent authorities to write these papers. In this number of *Arctic* we are including the first two papers to be received for the volume: "Some botanical problems of the arctic and subarctic regions" by Dr. Hugh M. Raup, and "Arctic and subarctic marine ecology: immediate problems" by Dr. M. J. Dunbar. The volume will be published as soon as all contributions have been completed. As the Institute feels that these papers are of immediate interest to readers of *Arctic*, we shall include additional papers as these are received.

SOME BOTANICAL PROBLEMS OF THE ARCTIC AND SUBARCTIC REGIONS

Hugh M. Raup*

The arctic and subarctic problems dealt with in this paper are primarily botanical. However, they are of such a nature that they require delving into many other phases of natural science, particularly surface geology, meteorology, and human geography. Consequently such problems as are suggested will have repercussions in these fields as well as in the broad field of biology. Within the field of biology my personal experience has been primarily in the study of vegetation, so that the problems I suggest will, inevitably, be weighted in that direction.

The solution of many problems in boreal biogeography will yield valuable and practically useful information for many purposes, civilian and military. The significance of these problems in the extensive use of arctic and subarctic lands by human populations lies first in the evidence they can give of the major geographic patterns or natural areas in the boreal regions. It is upon these major patterns that the outlines of use must eventually be based. This is an old concept which has been used with varying degrees of intensity and precision during the opening of the Western Hemisphere to European occupation, and the idea is still a good one. Its application is no longer simple, however; and in the hands of modern, highly trained specialists it can be badly misused. In earlier times it was successfully applied by broadly trained naturalists such as Douglas, Richardson, Macoun, and many others. It depends for its successful use upon what might be called correlative thinking in the natural sciences, and this type of thinking has become rather rare in these days of extreme specialization.

A second system of application is a refinement of the first. It involves the use of the natural vegetation in its relationship to local environments to indicate the cultural capabilities of the land. A third application is of large military significance. It involves the use of vegetation as an indicator of the "kind of ground".

All of these applications of botanical science to the intelligent use of the land depend upon a knowledge of the vegetation in all its aspects. Such knowledge is still in its infancy for most of the arctic and subarctic regions.

It is possible to make a general subdivision of northern vegetational problems into two groups, though the division is not a natural one and is to be used only for convenience.

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Floristic problems

The basic floristic problem in boreal North America is the development of a comprehensive, descriptive flora, with keys and illustrations which will aid in the identification of plants. No such comprehensive flora now exists. The last one attempted was more than a century ago. At present we are dependent upon regional lists of species, and upon a great mass of miscellaneous papers embedded in periodical literature.

The Eastern Arctic is pretty well covered by Nicholas Polunin's 'Botany of the Canadian Eastern Arctic,' Parts I and II. These papers cover the region from northern Ellesmere south to the 60th parallel. They do not, however, cover the Western Arctic islands or go much beyond the western coast of Hudson Bay, and they do not include Greenland.

My own published work covers the central and southern portions of the Mackenzie drainage basin. In the western parts of boreal America the only comprehensive work is that of Dr. Eric Hultén on the flora of Alaska and Yukon. This has been published in parts, and is now complete. The final part of J. P. Anderson's 'Flora of Alaska and adjacent parts of Canada' was issued in April 1952. Of the above papers, only those of Hultén and Anderson contain keys for the identification of the plants. Erling Porsild of the National Museum of Canada has a manuscript flora of the Canadian Western Arctic, and has recently published a critical and comprehensive treatment of the vascular flora of southeastern Yukon adjacent to the Canol Road.

All of these papers are, of course, based upon such collections of plants as have been made to date. They cannot be regarded as complete in any sense, for there are vast areas in boreal America where botanical collections have never been made. Such fundamental field work is necessary in the Western Arctic islands and particularly in the interior portions of all the larger Arctic islands. Our present knowledge of most of these islands is based upon collections made at relatively few points on their shores. The same is true of the interior of the Labrador-Ungava Peninsula and the interior of Keewatin. Even south of Keewatin there are large botanically unexplored areas in northern Manitoba and northern Saskatchewan. There are huge areas in western Mackenzie, northern Alberta, northern British Columbia, and Yukon that remain to be explored. The same is true, of course, in Alaska, particularly in the mountain and plateau regions away from the main routes of travel.

The development of plant ranges and patterns of distribution will remain uncertain and incomplete until this exploration is much further along than it is now. In planning and carrying out the work, it is essential that trained men should be engaged in it. The number of persons who have collected plants in boreal America during the past century and a half is legion, but it is safe to say that not more than a dozen of them have been able to do anything that would remotely resemble a comprehensive job. If the amount of money and time that has been spent in this pursuit over the years could have been concentrated in the hands of a few well trained people, the job would have been done long ago.

In order to be a good collector, a man has to know a great deal about plants and the way they differ from one another. This can only be got from training and experience. It has been a prevalent misconception, persisting for generations, that anyone given a plant press could collect the flora. Most of the money and resources that have been spent under this misconception have been wasted. We should set out systematically to cover the area, first on a regional basis. Then all the collected materials and information should be concentrated in one place, or at least in the hands of one man who would be competent to put it together in a usable form.

This project is placed first because it is necessary to produce the grist before the phytogeographic mill can be operated profitably.

The plants which occupy a given spot in boreal America are there because they were available when a place was opened to them, because they had the capacity to move into the place when it became available, because they had the capacity to adjust themselves to the physical and biotic limitations presented by the situation, and because they were able to reproduce themselves there. It is quite obvious that simple analyses of climate and soil will not explain the occurrence and behaviour of the plants that are found in a given place, and it is necessary that the identities and geographic origins of the plants be taken into consideration, as well as migrations and adjustments in time and space.

Vegetation is composed of individual species of plants, each of which has a population that varies widely in numbers from place to place, and in prominence and significance in the total plant cover. Each of these species has had a complex evolutionary history, and now contains genotypes that are the result of this history and of the various vicissitudes that the species has been going through during its history. Within its population these genotypes are commonly not evenly distributed, so that the behaviour of the species in one region will give no indication of its behaviour in another. In one area it may be predominant in numbers and in influence upon the total vegetation, and in another it may be reduced to insignificance. Herein lies a mass of problems in the nature of species—problems that are of fundamental significance to the study of vegetations and ultimately to their significance in the use of the land. Experimental studies in the genetics of boreal species, carried on in the field, are at the base of these problems.

This can be illustrated with the common white spruce, the most important timber tree in the subarctic forest. It is generally recognized as a single species ranging from Newfoundland to Alaska. It contains at least three separate entities which differ in general appearance, in local habitat selection, and probably in the quality of the wood. The most easterly form ranges westward into Saskatchewan, and probably into northern Alberta. It is a tree of moderately drained upland soils and flood plains. Another form ranges through northern British Columbia, northern Alberta, southern Mackenzie, south in the Rocky Mountains, and northwestward into Yukon and Alaska. It is the so-called "Alberta spruce", and has a much wider range of habitat selection than the eastern spruce. I have found it on high mountain slopes, on dry sand plains, and in muskegs. There is a great variety in the quality of its

wood, though, so far as I know, no one has ever made comprehensive tests of these qualities. A third phase of the white spruce grows in Yukon, northern Mackenzie, and parts of Alaska. It has only recently been described, and its range and characteristics are only partially known. It appears to be quite limited in the range of its habitat selection, growing on gravelly terraces and glacio-lacustrine deposits. I have also found it on dry south-facing mountain slopes. I think I am safe in saying that nothing whatever is known about its timber qualities, or its genetic origin. Workers in western Alaska are turning up still another spruce, which may or may not be a separate strain.

These spruces are sufficiently well known to indicate a pattern of distribution, and we know that they differ superficially. Beyond this we have nearly everything to learn about them, except that we know the timber values of the eastern form and something of the values of the Alberta spruce. This kind of problem can be multiplied by the hundreds in the boreal flora. In detail it has all the aspects of a problem in pure science, but it can have immediate repercussions in the practical use of the northern lands. It will require for its solution not merely a working knowledge of taxonomy and genetics, but also of the whole gamut of geological and meteorological changes that have affected boreal North America during and since the Pleistocene. Corollaries to it are broad problems of speciation in all of the boreal parts of the world, such as the occurrences and distribution of endemism, polyploidy, apomixis, and the like. The broad outlines of some of these problems are beginning to take form, but we are only at the beginning.

It has been suggested above that the ultimately useful units in the flora may not be the units that will be recognized by the taxonomists who develop the "Flora", because of genetic variations within the species. In key situations, therefore, experimental studies in the nature of certain species should be initiated *in the field*. Some of these experiments will be comparatively long-term affairs, and will have to be established at bases that can be continued for some years. There are plenty of establishments throughout the boreal regions which could be used for such purposes, given funds for necessary adjustments or reorientations.

Men of special training in practical genetics will be necessary for this work. They should be men who are broadly trained in botanical science, rather than one-sided students of plant inheritance, for it will be necessary that they understand something of the broad significance of what they are doing. They must be content to spend long summer seasons at relatively isolated stations. It is only from such work that we will learn how the taxonomist's species have been put together during glacial and postglacial time.

The history of vegetation involves the study of plant fossils which, in the present problem, involves the study of peat. Very little is known of geologically rcent peat deposits in the north. One of the reasons for this is that the peat is frozen and cannot be sampled as easily as that in temperate regions. The study of peat deposits in the north involves to a considerable extent an engineering problem. It is essential, however, that it be done if we are to understand the geographic patterns involved and to make them useful.

Problems in plant communities

A second great complex of problems relating to the plant cover is in the study of the masses of vegetation which are made up of the various species. In this field some of the main outlines of geographic distribution have been known for a long time. The boundaries between the tundra and the forest, whether on the northern interior plain of the continent or on the mountain slopes, are relatively well known. One of the great natural boundaries in the world's vegetation is between the northern forest and the tundra. At present, however, this boundary is little more than an observed fact, for we do not have a clear idea of why it occurs where it does. It is presumed to reflect a climatic boundary, but how the climate differs on either side of it, and how the difference affects the growth of trees is very little known.

A primary characteristic of vegetation in the mass is that it is extremely unstable. It undergoes changes which may be due to influences external to itself, such as alterations of climate and soil. It is also affected by the results of its own existence on a given area, because in itself it alters the soils and the microclimates. It is also subject to modification, especially in the arctic and subarctic regions, by the influx of species from other regions, and by the effects upon it of grazing and other animals. The resultant of all these changes, both internal and external, is the vegetation on the ground at any point in time. It follows that the significance of vegetation as an indicator of the kind of ground, or of the usability of the ground for agriculture or silviculture rests upon an understanding of the rate and kind of changes that are occurring. Here are some of the most important problems in the boreal biota, and here again we are only at the beginning of the necessary understanding. Here also are excellent examples of failure due to extreme specialization on the part of field workers. Far too many of the students who have undertaken to use the vegetation for its indicator values in the north have failed to take into consideration its quality of instability.

The difficulties in the use of natural vegetation in the north for its indicator values are manyfold greater than they are in temperate regions, because the very base for interpretation is a new and little understood one. In temperate regions the development of vegetation is very closely related to the development of land forms under the influence of subaerial erosion. The fundamental concept here is the "cycle of erosion" by running water. Land surfaces are uplifted by orographic movements, stream gradients are increased, water tables are lowered, erosion is stepped up, and new flood plain deposits are formed. Vegetation on the uplifted surfaces is altered or destroyed, and develops on new deposits. Other effects related to this occur on beaches subject to wave action, or on dry surfaces subject to wind action. On the aquatic side, ponds and lakes are physiographic features that are made or reduced by surface changes due to erosion. Out of these complexes we have developed what is known as the "physiographic ecology" of vegetation.

In the arctic and subarctic regions subaerial erosion is often a minor factor in the degradation of land surfaces, and the slow movement of surface materials

under the influence of frost is of primary significance. The effects of frost action on the details of surface configuration, and their significance in the moulding of larger surfaces, are just beginning to be known. Each year that geologists work in the Arctic they turn up new aspects of these processes. The development of vegetation there must be related to a developing knowledge of surface changes under the influence of frost. In short, a new brand of physiographic ecology must be written. Botanists are now making a fine beginning in this field.

It was said above that the indicator values in northern vegetation cannot be interpreted from simple observations at given points in space and time, because the vegetation is not a dead blanket, but rather it is an unstable, developing, biotic phenomenon. The whole plant cover of the boreal regions must be studied and interpreted in this light if it is to be significant for purposes other than immediate utilization. Attached to many kinds of parties engaged in field operations, whether they be in photo-interpretation, geological investigations, engineering reconnaissance, or agricultural and forestry reconnaissance, there should be men who are especially trained to interpret vegetational change. These men, again, should not be too highly specialized, for they must have a working knowledge of floristic geographic phenomena, and they must understand the relationships between vegetation and climate and soil. They must have a working knowledge of the evolution of soils and land forms, and of the occurrence and significance of microclimates and of climatic change. Of all the men in the field, these will be the most difficult to find, for our system of training students of vegetation during the past fifty years has not produced many of the kind that is necessary. On the other hand, the study of vegetational change involves many disciplines which can be applied by specialists provided there is adequate direction and correlation.

Arctic vegetation bristles with problems relating to the physiological relations between the plants and their environments. Water relations in arctic vegetation are very poorly understood, as are those involving the availability and use of mineral salts. The nitrogen cycle in arctic and subarctic regions is particularly worthy of investigation. However, I do not believe that these physiological problems should be stressed until much more basic work on the geography of the plant life has been done. A certain amount can be accomplished by men who are versed in the intricacies of such problems and who can be attached to field parties, but far too much physiological work has been done without reference to the basic facts of the identity and natural occurrence of plants. This work now stands alone and probably can never be fitted into a natural context of vegetation. Physiological research on arctic plants must somehow be carried into the field, out of the laboratory. The progress that has been made by the group working at Point Barrow is encouraging.

The use of lands for agriculture, grazing, or timber production in the American North is in its early stages. My own studies indicate that frost and the short growing season in most parts of the Arctic and Subarctic are not so significant in this connection as is the shortage of water. Whoever

attempts to develop northern land should approach the problem with a completely open mind, trying many kinds of plants, in many kinds of sites, and by many modifications of the existing growing conditions.

The following is an outline of problems derived from the above discussion:

Botanical exploration

1. Floristic exploration:
   Western Arctic islands
   Interior of Arctic islands
   Interior of Labrador-Ungava Peninsula
   Interior of Keewatin
   Northern Manitoba and Saskatchewan
   Western Mackenzie
   Eastern and northern Yukon
   Northern British Columbia
   Mountains and plateaus in interior Alaska.
2. Description and analysis of plant communities:
   Needs to be done in most of the boreal regions.

Flora of boreal America

3. Preparation of a comprehensive "Flora", with keys and descriptions, preferably illustrated.

Origin and distribution of the flora

4. Preparation of range maps of species.
5. Investigation of genetic variability in species as related to their geographic behaviour in Pleistocene and post-Pleistocene time.
6. Relation of species distribution to development of landscapes.

Origin and distribution of plant communities

7. Relation of development of plant communities to development of arctic and subarctic land forms, particularly with respect to cryoplanation.
8. Reconstruction of post-Pleistocene landscapes, both as to morphology and biota.
9. Investigation of the concepts of "succession" and "climax" as applied to boreal vegetation.
10. Relation of climates, both local and general, to the nature and distribution of vegetation.
11. Effects of man and other animals upon the vegetation.
12. Effects of fire upon native vegetation.
13. Studies of peat deposits and other fossil remains.

Problems in applied botany

14. Sustained yield utilization of native forests and grasslands.
15. Investigation of agricultural expansion.
16. Interpretation of vegetation as an indication of "kind of ground".
17. Interpretation of air photographs for the mapping of natural resources and "kind of ground".

ARCTIC AND SUBARCTIC MARINE ECOLOGY: IMMEDIATE PROBLEMS

M. J. Dunbar*

THE study of marine biology in the north has been pursued, in the past, mainly by the Scandinavian countries. In the northern waters which Scandinavian biologists do not normally visit, and especially in the North American Arctic, marine investigation is in its infancy, and has even lagged behind terrestrial ecology in the same area. As there are now signs that this condition is to be put back in balance, this is the proper time to review briefly the most interesting results of the past and to point out the most promising fields of study for the immediate future.

For the purposes of this paper the terms "arctic" and "subarctic", applied to the marine environment only, are used as defined previously (Dunbar, 1951a): the marine arctic being formed of those areas in which unmixed water of polar origin (from the upper layers of the Arctic Ocean) is found in the surface layers (200–300 metres at least). Admixture of water of terrigenous origin is ignored in this definition. The marine subarctic is defined as those marine areas where the upper water layers are of mixed polar and non-polar origin. By far the greater part of the marine subarctic lies on the Atlantic side, extending from the Scotian shelf and Hudson Strait to the Barents and Kara seas, and including almost the whole coast of west Greenland, the waters around Newfoundland and Iceland, much of the Norwegian Sea, and the waters off the west coast of Spitsbergen. The southern boundary of the marine subarctic is the limit of southward penetration of the arctic water; clearly it varies seasonally and with the state of the climatic cycle. For the large and rather ill-defined marine region south of the subarctic, the term "boreal" is used here, but with that region we are not directly concerned. It should be added that the division employed here apparently applies less to sessile animals and plants, than to the plankton and nekton, because of local variations in summer. This does not disturb the general picture, and is discussed further below.

Production

The fact that this division between the marine arctic and subarctic is not an arbitrary thing, but reflects a real and obvious difference in the biological production of the two regions, points to this difference as one of the most interesting things about the northern waters, and the study of the causes of the difference has only just begun. The fact itself is quite evident: the great subarctic belt across the North Atlantic area is one of the richest parts of

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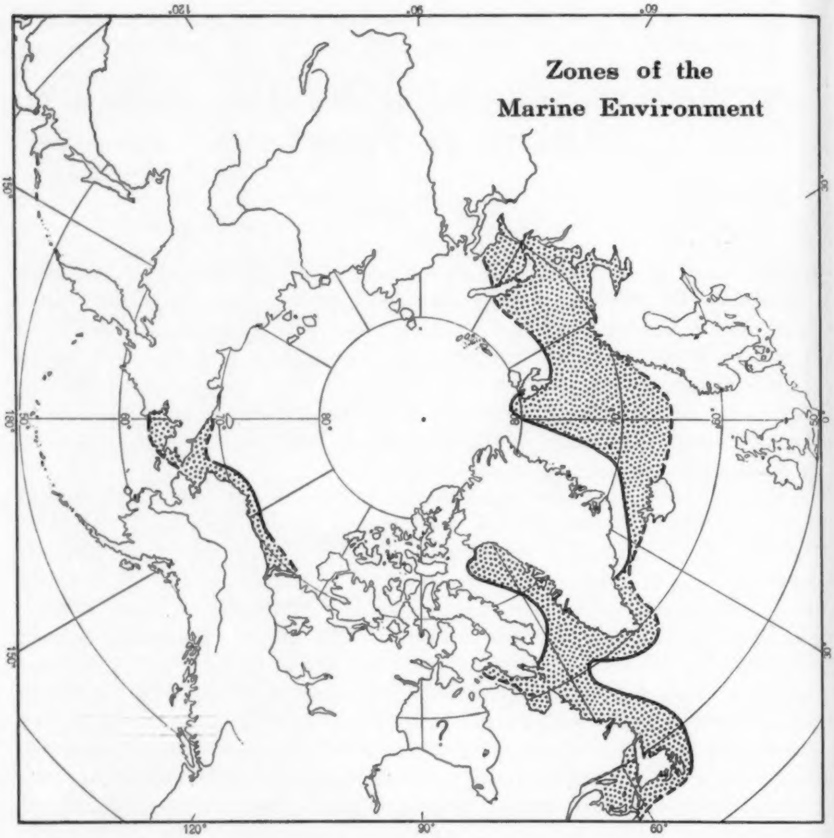

Fig. 1. Zones of the marine environment; the subarctic zone, as defined in the text, is stippled. The lines of delimitation are approximate, and dotted lines indicate regions still in doubt. There is some evidence that the subarctic should extend farther south in the region southeast of Iceland, northern Scotland, and western Norway, and that the coasts of Kamchatka and parts of the Seas of Okhotsk and Japan should also be included in the subarctic.

the oceans of the world, the home of fisheries of immense value, maintained by many nations of the Atlantic community. That these fish resources are dependent upon plankton production is obvious, and the same is true of other parts of the seas of great economic value, such as the subantarctic belt and the region of influence of the Peru Current off the west coast of South

[1]Figures 1 to 4 are reproduced from drawings prepared for the author's chapters on "Northern Waters" in the forthcoming volume 'Geography of the Northlands', edited by G. H. T. Kimble and Dorothy Good, to be published for the American Geographical Society by John Wiley and Sons.

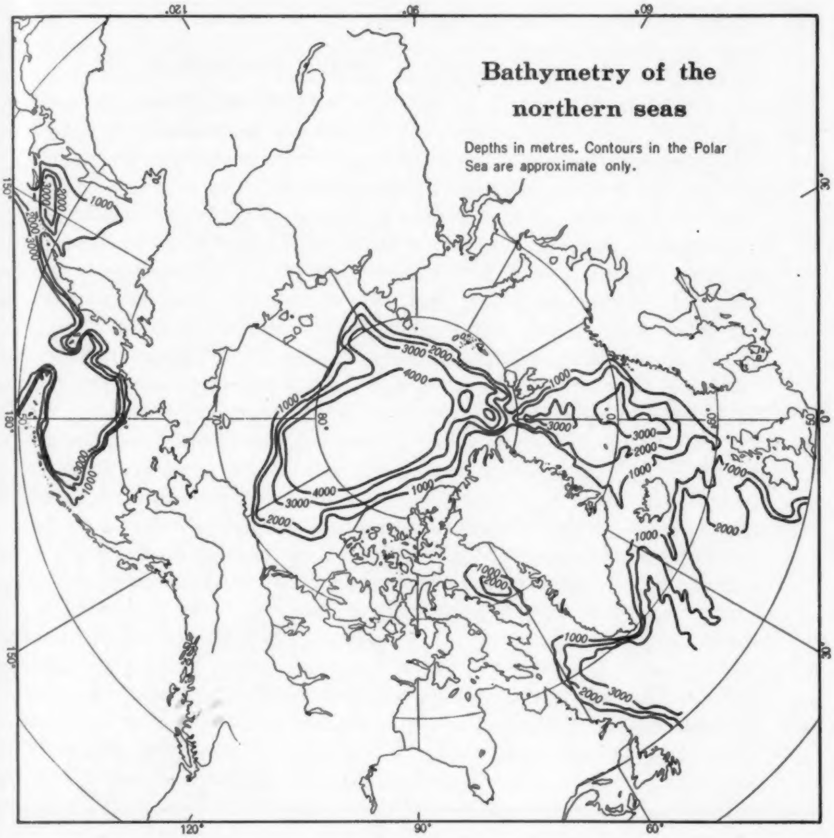

Fig. 2. Bathymetry of the northern seas. The four deep enclosed basins (Arctic Ocean, Greenland and Norwegian seas, and Baffin Bay) have many faunistic points in common, although separated by submarine ridges. Notice the Wyville Thompson ridge north of Scotland and its extension to Iceland and east Greenland, also the similar ridge in Davis Strait. Both ridges rise to a water depth of about 600 metres.

America. In fact the much higher plankton production in the subarctic, when compared with the arctic, is at once apparent in the field. The quantitative measurement of this difference in production, however, is only now beginning in certain parts of the north, and is one of the next steps to be taken in the North American Arctic and Subarctic. The chemical and physical factors underlying the differences in production have also to be investigated. It may be that the high production in subarctic water is caused simply by the lifting of the temperature inhibition in water of arctic origin (arctic water being very cold, and therefore presumably a depressant upon

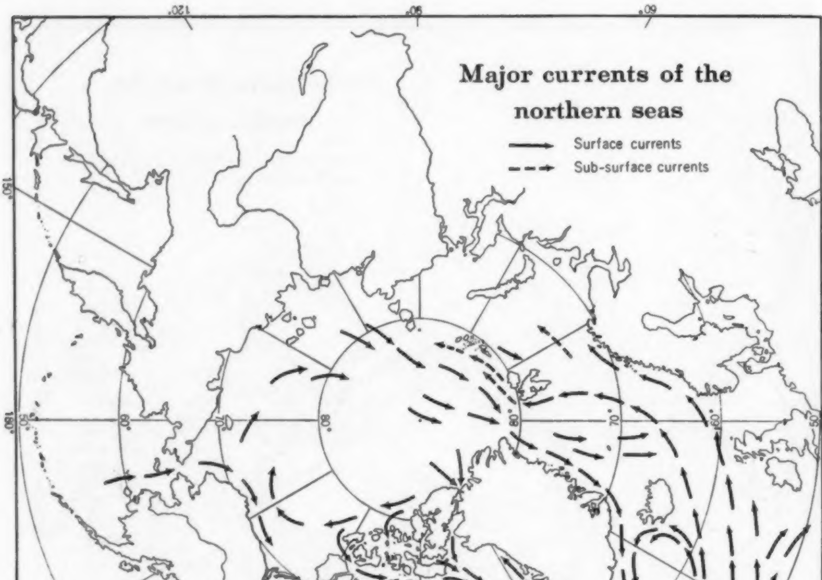

Fig. 3. Major currents of the northern seas. All details, lesser eddies etc., omitted.

growth rates[1]), which is otherwise of high production potential in such properties as gases held in solution, nutrient salts, and high viscosity; but this has still to be demonstrated. It has also been suggested that the presumed high concentration of polymerized water molecules (trihydrol or higher polymer) in water recently melted from ice may have a beneficial effect upon the growth and division of plant cells, as has been demonstrated experimentally. So far no method of measuring the concentration of specific water polymers has been devised.

[1]It has been demonstrated that the growth rates of the larvae of certain bottom-living forms in the arctic and subarctic are in fact no lower than in similar species in warmer water, indicating presumably a genetically established regulating mechanism, but for the mass of the zooplankton, and for the phytoplankton, there is as yet no evidence of this. In fact, the much larger generation time in colder water in the holoplanktonic animals, indicates a greatly reduced rate of growth. For the pelagic larvae of benthonic species there are other pressing considerations which favour the selection of the higher growth rates, and which do not apply to the holoplanktonic forms.

There is another possibility in this matter of subarctic production which requires testing, namely that the high production is caused entirely by upwelling of water from lower layers, laden with plant nutrients, at all times of year. Thus the underlying cause of the high production in the Icelandic waters, and in the vicinity of the Faeroes and northern Scotland is, on this view, the presence of the submarine ridge (Wyville Thompson ridge), running from Scotland to the Faeroes, and extending from there to Iceland and east Greenland, causing upwelling of Atlantic water. The ridge between Holsteinsborg and southeast Baffin Island is supposed to play the same part in southwest Greenland. High production in the subarctic belt is thus looked upon as strictly comparable to the high production along the west African coast and the west coast of South America, although the types of water upwelling are markedly different. In the latter two regions it is cold antarctic water which comes to the surface, whereas any upwelling in the Iceland–Scotland area must be of Atlantic water. Again, it may be that the mixture of polar and non-polar water causes general instability, favouring vertical exchange of water, and that this is the important thing in determining subarctic production. It is of course clear that upwelling, wherever it occurs, will normally increase production, as it does everywhere in the usual annual succession of events. But it is still doubtful whether upwelling alone can explain the high subarctic production; it is significant that wherever arctic water meets boreal water, the production goes up. Moreover, it is by no means demonstrated that instability in subarctic waters is the rule; there is high stability, for instance, in the west Greenland coastal current in summer.

Quite apart from further hydrographic work designed to show the stability or instability of subarctic waters, and the extent of upwelling, the measurement of the phosphate and nitrate concentrations in both arctic and subarctic water should go far towards elucidating this interesting matter, the discussion of which dates as far back as Nansen (1902) and Gran (1902). The problem was attacked by Braarud (1935) in Denmark Strait and the east Greenland current, but it is not yet quite clear to what extent the supply of plant nutrients in the surface layers is exhausted during the phytoplankton bloom, and how soon it is replaced. It is quite possible that the phosphate is not exhausted in the arctic water in the spring, and that the arctic water may always have a significant surplus of phosphate and nitrate to contribute to the subarctic, even in summer.[1] The Russian Papanin expedition of 1937 found that although the phytoplankton growth in the Arctic Ocean in July was poor, there was considerable flowering in August, by which time the snow cover had melted and the penetration of light became possible. The presence of considerable quantities of phytoplankton beneath the ice in summer is also recorded from Point Barrow (MacGinitie, 1949, personal communication). If the use of the plant nutrients occurs so late in the season in the Arctic Ocean, it may well

[1]Measurements of phosphate by the *Dana* expeditions of recent years have shown low values, down to zero at the surface in July, in east Greenland. Measurements made by the *Calanus* expedition, however, in Cumberland Sound, Baffin Island, show somewhat higher values, and the *Godthaab* results were variable. The question is by no means settled.

follow that the outflow of nutrients in the east Greenland current and through the Canadian Archipelago in the spring is quite large.

The measurement of the amount of plankton can be done in several ways. The number of plant cells can be counted directly from samples collected in water samplers and preserved in weak formalin, a method which was used by Gran (1929) and by Braarud (1935), and which is at present being employed by Grøntved (1953, personal communication) on samples from west Greenland, with good results. The zooplankton, excluding the largest members, is measured by the use of vertical nets, or by quantitative mechanical sampler. Both these methods measure the "standing crop", or concentration of organisms at a given time, and they are reliable if enough samples are taken. Chemical methods, measuring the consumption or production of a given element of metabolism, provide an estimate of the rate of production; a recent innovation in this field is the Carbon-14 method developed by Steemann Nielsen (1952) and used on the *Galathea* expedition. All these methods should be applied to the North American Arctic and Subarctic.

There are particular areas where such study of the plankton production would be of special interest, such as Hudson Bay, the Arctic Ocean itself, and the Beaufort Sea. The latter, although strictly speaking a part of the Arctic Ocean, is nevertheless clearly influenced by non-arctic water from the Bering Sea. Hudson Bay is highly stratified in summer, and it has been supposed that the apparent low production of the Bay (which still has to be confirmed) is caused by the lack of proper vertical exchange of water during the winter. There are thus two points to be cleared up in Hudson Bay: the actual level of production of living matter, and the winter hydrographic regime. The latter can of course only be done by working stations through the ice, a technique which has already been tried out on several occasions: by the Danish Three Years expedition in east Greenland (1931–4), by the Papanin expedition of 1937, by Digby at Scoresby Sund, and by Nutt in the Goose Bay region in 1952. A technique of through-the-ice work is described and illustrated in Thorson's (1946) most useful paper on future work in arctic animal ecology.

The plankton production in the Arctic Ocean itself has been a matter of contention for many years, but it has never yet been measured. Nansen, after the famous *Fram* expedition of 1893–6, concluded that the Arctic Ocean was a barren area, because his plankton nets caught little plankton and the seal population seemed very low. Stefansson, on the other hand, having lived on seal during a prolonged trek across the polar ice during the Canadian Arctic expedition of 1913–8, obtained a quite different impression, and reported, moreover, the abundance of so-called "shrimps" (possibly a pelagic amphipod) in the surface water between the ice floes. The collections of the Russian Papanin expedition of 1937 apparently confirmed Stefansson's conclusions rather than Nansen's, although the final plankton results do not seem to have appeared yet. Clearly this situation calls for decisive study, and the only way to do it is to maintain regular quantitative plankton collections all year round at one station, chosen for ease of access and depth of water. Probably the coast of northern Ellesmere Island, or of Greenland, offers the best conditions.

The penetration of light at all seasons of the year, and the oxygen and phosphate concentrations, should of course be measured at the same time.

Before leaving the subject of production, mention should be made (1) of the necessity for study of winter as well as summer conditions in all phases, both in those areas normally frozen over, and in the ice-free subarctic regions of southwest Greenland, and (2) of the need for bacterial studies in northern seas, in order to establish the rate of bacterial mineralization of organic detritus.

Plankton biology in general

There are other facets of plankton biology in cold waters which offer valuable returns for research, but which can be mentioned here only in summarized form:

(1) Vertical diurnal migration of the plankton, a normal phenomenon all over the world and largely dependent upon changes in illumination, was observed in Svalbard waters, latitude 80°, in 1893 by Walther, even in the height of summer when the sun was well above the horizon at midnight. Walther was surprised to find this phenomenon so far north in summer, but Russell (1927) has since pointed out that the illumination which is able to penetrate the surface at that latitude in June, at midnight, is very much less, midnight sun or no midnight sun, than the penetration at noon. Later, however, Bogorov (1946) published his observations in the Barents Sea, in which he found no evidence of vertical migration during the height of summer. Clearly this problem needs further research.

(2) Cold-water plankton is remarkable for the large size attained by the individuals, when compared with the same or closely related species in temperate or warmer waters. It has been assumed that the effect of the low temperature on the development of the gonads is one important factor: "Delayed sexual maturity, which favors growth in size, appears to be directly dependent on retardation of growth at lower temperatures, and this is a common characteristic of northern marine creatures" (Hesse, Allee, and Schmidt, 1937, p. 159). It is not yet clear, however, why the gonadial growth does not maintain the same rate, relative to somatic growth, as in warmer water. It may be that so much energy is required to offset the very low environmental temperatures that the gonads are penalized in favour of the general metabolism. Large size is an advantage at low environmental temperatures, for poikilotherms as for homoiotherms, but in poikilotherms it requires a longer life to achieve it (relative to the size of the species), because growth rates are controlled by the environment (see footnote p. 78); the adjustment of the gonadial and somatic growth rates may therefore be established in the hereditary mechanism of the species, and may not be simply and directly controlled by the external temperature. At all events, in order to throw light on this perennially puzzling matter, an investigation of the metabolism of arctic plankton animals is needed. The measurement of the oxygen requirements of arctic plankton could be done quite simply in an adequately equipped ship's laboratory, but more simply in a shore station. The results would

dovetail usefully with the work of Thorson (1936), who studied the oxygen metabolism of shallow-water benthonic forms, mostly molluscs, in northeast Greenland, and found that the metabolic rate was approximately the same as in closely related temperate (Danish) species and in tropical species, each group being measured at their normal environmental temperatures. Measured at the same temperature, the arctic forms showed a considerably higher metabolic rate. The whole matter of body size and metabolic rate has recently been reviewed, with considerable new experimental work, by Zeuthen (1947), and a theoretical development of the question has been published by Hemmingsen (1950).

(3) Thorson (1946, p. 25) mentions the food of zooplankton in the north as requiring research. To quote one point from his paper: "Ussing [1938] is of opinion that in winter most copepods [in east Greenland] are able to live on the food obtained in summer (stored as oil drops). Place, therefore, such winter-copepods in sterile sea-water to have this problem cleared up." This work, together with the metabolic study already mentioned and other research discussed below, needs wintering parties with laboratories equipped with constant temperature aquaria, filtering devices, and so on. Laboratories aboard research vessels, even small vessels, should also be similarly equipped if possible.

(4) Breeding cycles of planktonic animals, the nature of which is fundamental to the production of the standing crop each year, require a great deal of study, and for best results also call for winter as well as summer work. The fact that interesting complications arise in the breeding cycles of certain zooplankters in the north has already been demonstrated by Dunbar (1941). Generation time in certain copepods has been studied by Ussing (1938), and the bimodal size-distributions in copepods found in northern waters by Ussing and by Jespersen (1934) are also involved in this matter of breeding cycles. The suggestion of Ussing that the surface water of fjords, which is warmed in summer time and which has been called "fjord water" by the Danish workers, is important and perhaps essential to the survival of arctic copepods, requires testing.

Benthonic and littoral fauna

Many benthonic and littoral animals are sessile, and all of them, except the fishes, are limited in powers of locomotion and dispersal. Most of them, moreover, are restricted in their distribution with respect to depth. These circumstances make it less simple to follow the arctic–subarctic pattern of distribution in the benthos and littoral than in the plankton and nekton. Large scale changes in the position and extent of the subarctic marine belt will of course result in extinctions of sessile populations and their replacement by others, but at any time during this climatic cycle there will always be seasonal differences in temperature in the upper 30–50 metres of water, which will greatly affect the distribution and living conditions of these forms. This has been pointed out and developed in a very interesting manner by Lemche (1941), for the opisthobranch gastropods of east Greenland. Forms of more southerly affinities are found in northeast Greenland in the upper waters only, where

reproduction can take place at less rigorous temperatures in the summer. Below this zone there is a population of arctic forms which live at the lower temperatures all year round. Consequently, if the distribution of the two groups are placed on the same map without taking depth into account, they are found to coincide almost exactly in east Greenland. This of course is quite misleading, and emphasizes the fact that for the division of the benthonic fauna into arctic and subarctic regions it is essential to allow for this differentiation within the upper water layers. (The criterion employed, described above, deals with the upper 200–300 metres of water, which is the approximate depth of the arctic water layer in the Arctic Ocean; below this the depth factor applies also, naturally, to the plankton). So far, no work of this sort has been done on the North American Arctic shallow-water benthos.

The distinction between the two groups just mentioned lies in their reproductive physiology, and there is no doubt that the most promising lines of research in this ecological division lie in the elucidation of the reproductive requirements and limitations. Dr. Gunnar Thorson, of the University of Copenhagen, has made notable advances in this field, and since he has already reviewed the whole subject on a global scale (Thorson, 1950; 1951), and also established the study in arctic waters (Thorson, 1936) and indicated the points which require research in the immediate future (Thorson, 1946), it is not proposed to deal with this subject here. It must be enough to point out that a valuable contribution to the whole pattern of benthonic reproductive habits, which are of great interest, would be made by applying Thorson's methods to the North American fauna, particularly as regards the presence or absence (and length) of the larval life. There is also much work to be done on the density of the benthonic fauna, by the use of bottom samplers, along the lines of Vibe's (1939) work in the Thule and Upernavik districts.

The term "littoral" is used here as coextensive with "intertidal", and thus not in the sense advocated by Hesse, Allee, and Schmidt (1937). The littoral fauna has special conditions to face, in which the atmospheric climate must play an important part. It was upon the marine climate, however, not the atmospheric climate, that the study of Madsen (1936; 1940) put the emphasis as possibly determining the distribution of northern littoral faunas. His work suggested that the littoral fauna in large part disappeared north of a point which was determined by the nature of the water, possibly by the presence or absence of Atlantic water on the coast. This point would thus coincide with the boundary between the arctic and subarctic regions as defined in this paper, and hence the nature of the littoral fauna might serve as an added indicator of hydrographic conditions. Before this possibility can be developed, however, a great deal of littoral collecting is necessary, especially in the North American Subarctic.

Apart from such zoogeographical considerations, the littoral fauna of the northern seas calls for investigation of breeding seasons and breeding cycles at different levels on the beach, and of the conditions of survival during the winter, on all of which points our knowledge is extremely poor. The biology

of such abundant forms as the amphipod crustacean *Gammarus* (several species), the barnacle *Balanus balanoides,* and the snail *Littorina saxatilis,* for instance, has scarcely been studied at all on arctic and subarctic shores; and almost nothing is known of the northern littoral microfauna.

Nekton (fishes and marine mammals)

It is in the study of the macrofaunal elements of the northern seas that we come into immediate contact with the economy of the Eskimo, and it is here that investigations intended to develop new resources, or to conserve the old, become of immediate value. They are not on that account necessarily the most important in the long run, but they appeal to the general public, and hence reach more easily for the public purse-strings than the more obscure scientific projects can hope to do.

In true arctic waters, that is, inside the arctic zone as here defined, fishes are not abundant, and the nektonic constituent in the biomass is dominated by the mammals; in the subarctic waters, fishes make up a very important part of the total fauna, and the mammals are not dominant. This interesting fact, which has as a corollary the direct dependence of the mammals, in the arctic zone, upon the macroplankton (invertebrate) instead of on the fish, has never been explained, nor has there been any attempt to throw light upon it experimentally. Speculation upon it leads to a consideration of the glacial history of the northern waters, and of the time-scale in the evolution of fishes, and although the problem of the glacial history can be attacked in various ways through the study of northern marine ecology today, it is not the purpose of this paper to develop this line of thought. It has been touched upon in another paper (Dunbar, 1951b).

The problem can also be attacked, more directly, by the study of the metabolism of arctic fishes at the temperatures at which they live, and of the general relation which their reproduction and development bear to temperature. It should be emphasized that the poverty of the fish fauna, in terms of numbers of fish species, is not itself surprising—it is part of the general picture of fewer species of most groups in arctic water.[1] What has to be explained is why no single species has been able to achieve a dominant or even an important position in the total fauna, in contrast to other poikilotherms, all of them invertebrates, many of which are extremely abundant in arctic water, such as certain amphipods, copepods, and molluscs.

[1] A recent study (Thorson, 1951) has thrown a new light on the matter of species numbers in the marine environment of the arctic, temperate, and tropical regions. For the intertidal and shallow-water invertebrates, it is the "epifaunal" species which increase greatly in numbers toward the tropics, the "epifauna" including all dwellers upon the surfaces of various substrates, such as rock, stones, coral reefs, and seaweed, whereas the numbers of species in the "infauna", mainly burrowing forms in the large uniform environment of sandy and muddy bottoms, are approximately the same in comparable environments in all three major zones, tropics to arctic. In the light of this, the poverty of fish species (and also of holoplanktonic species) in the arctic water appears to be a breach of the rule, for ecologically the fishes, especially the pelagic fishes, must be compared with the benthonic and littoral "infauna", for which the environment is constant over large areas, and not broken up into a multitude of small habitats as in the epifaunal environments.

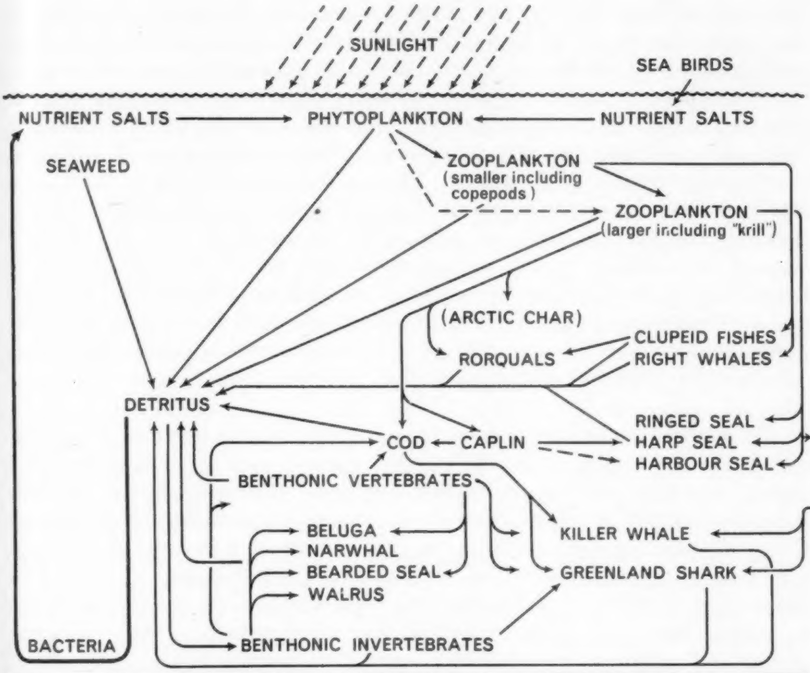

Fig. 4. The biological cycle in the arctic and subarctic marine zones, somewhat simplified. The prey–predator system illustrated in the right-hand three-quarters of the figure ends finally in the production of organic detritus, which is decomposed by the bacterial action mainly on the sea-floor in moderate depths. The resulting supply of inorganic plant nutrients (nitrates, phosphates) is returned to the surface by vertical water exchange in the autumn and winter, and is thus available for the regeneration of the phytoplankton population in the springtime conditions of increasing sunlight.

The poverty of the fish fauna in arctic water is particularly remarkable in the pelagial, as opposed to the littoral and benthal, regions. The polar cod, *Boreogadus saida*, although frequently referred to as a pelagic form because it is often seen among ice floes, is in fact much more commonly found close to the bottom in fairly shallow water; and the arctic char, *Salvelinus alpinus*, although in part a planktonic feeder during its short annual stay in salt water, cannot be considered a true pelagic species on that account. The shallow water benthos includes a few families of fishes which are widespread although nowhere very abundant. The young of these benthal forms, Cottids, Liparids, Agonids, Gadids, etc., are often taken in plankton nets, especially at night, and it is probable that much more could be learned about their abundance and their habits by the use of large (two-metre) stramin nets, and other types of small-mesh mid-water trawls. Pelagic young fish escape, for the most part, from the ordinary plankton nets. The same is true of the largest pelagic

crustacea, such as the Hyperiid amphipods and the Euphausids which, like the young fish, lie on the border-line between the plankton and the nekton, and which can be collected adequately only with appropriate mid-water trawls.

The subarctic fisheries must be left out of the present paper; they are an extremely large subject in themselves. Moreover, they are being studied and developed constantly, in such areas as west Greenland, Spitsbergen, and the Norwegian, Barents, and Kara seas. There is room for considerable biological work on the economic fishes of the Labrador coast, however, and the possibilities of the Beaufort Sea have yet to be investigated fully. At the northern edge of the subarctic water, and also beyond it, there is a need for experimental fishing for such forms as the arctic halibut, *Reinhardtius hippoglossoides*, and the Greenland shark, *Somniosus microcephalus*, in Baffin Island waters and northward. In the Burwell area of Ungava Bay the *Calanus* expeditions recorded the young of the arctic halibut, but the adults have not yet been taken.

In terms of man's immediate interests, there is an urgency about the scientific study of the arctic and subarctic marine mammals which does not apply to any other marine problem discussed here. The northern sea mammals have been hunted by Eskimo and by Europeans for centuries; the European killing has been for a shorter time, but has been very much more destructive. The Eskimo, by themselves and uninfluenced by Europeans, had struck a natural balance between themselves and their sea mammal resources. They were themselves part of an established ecological system. The commercial whalers and sealers, on the other hand, came from another system upon which they were dependent, and their activities among the northern sea mammals may rightly be termed an invasion. As might be expected, the species which they prized most, the Greenland whale or bowhead, was soon brought to the verge of extinction, and the introduction of the rifle to the Eskimo, by both whalers and traders, is now doing considerable damage to the seal populations. Whatever recriminations may be made about these two facts (the one is history, the other is now much more than a simple zoological problem), they have left problems which the zoologist can certainly tackle.

It is probably true that all marine mammal species in the north, at one or more points of their range, are now seriously reduced in numbers. There may be exceptions to this, for instance the white whale and the narwhal, which possibly are holding their own, but in general the marine mammal populations have been declining, and in a belated awareness of this, we are faced with the fact of our almost complete ignorance of the most elementary matters of their life histories. The cases of the Greenland whale and the walrus are particularly clear. Since the almost complete extinction of the bowhead before the First World War, it has been given protection, and there are signs now that the population has been very slowly increasing; for the present there is little to do about it except to leave it in peace, and to keep records of its recovery. But the walrus is another matter; there is clear evidence that the walrus was once much more widespread than it is at present, and it is improbable that this retreat has been caused entirely by changes in climate during the last four

hundred years, although that may have had something to do with it. The walrus has been the object of commercial hunting for several centuries, and it is still occasionally killed in numbers by sealing vessels. It is also hunted by Eskimo armed with rifles, some at least of whom seem to have forgotten their fathers' hunting wisdom, so that there is much waste, especially in summer, which would not have occurred in earlier times, and without the rifle. The same is true of other Pinnipedia in the north. The sinking during the summer hunting, caused by shooting the animals from a distance, very often without adequate means of retrieving them, accounts for the wastage of a ridiculously large proportion of the seal and walrus. It would be a mistake to think that this matter does not come into the business of the marine biologist. The Eskimo is part of the marine system, just as the whaler is, and his activities are most important zoologically. In this connection, the designing and introduction of a good, inexpensive shoulder harpoon gun would be helpful.

We have to make a study of the life histories of the marine animals, beginning from almost nothing, in order to discover where we may apply conservation measures. A little has been published on the walrus, from Alaska (Collins, 1940) and from northwest Greenland (Vibe, 1950), but for the rest we have only scattered observations published in odd corners of expedition reports, popular books, or filed in manuscript in Government offices. There is an excellent account of the harp seal (*Phoca groenlandica*) of the White Sea area by Sivertsen (1941), and Fisher (1952) is conducting a thorough study of the harp seal on its Gulf of St. Lawrence breeding ground, sponsored by the Fisheries Research Board of Canada. The harp seal, like the hooded seal (*Cystophora cristata*), is a migrant species, spending the summer in the north. Those which breed in the Newfoundland and St. Lawrence area move to west Greenland and Baffin Bay in the spring, and they are fairly common in Ungava Bay and along the eastern and northern coasts of Baffin Island. It is in this northern part of the harp seal range that we need information on abundance, food habits, and migration. It is possible that some of the adolescent seal remain in the north during the winter; if so, it is important that we have some estimate of the numbers involved, in order that population studies done farther south, in the breeding areas, may take this into account.

For those sea mammals that breed in the north—walrus, ringed seal (*Phoca hispida*), bearded seal (*Erignathus barbatus*), and some of the harbour seal population (*Phoca vitulina*), also the beluga or white whale and the narwhal, a program of research should include the following: (1) A census done by counting breeding colonies, summer schools, hunting kills, and by running counts from ships in transit, all of which must be kept up through the years. (2) The collection of reproductive tracts, stomach contents, and parasites, in sufficient numbers to give good material for laboratory study. (3) The collection of teeth and possibly certain bones (bacula, for instance) for ageing purposes, so that the age composition of the population may be determined; and the discovery of good methods of ageing in general (the use of teeth is quite new for seal and walrus, and there may be other means). (4) The study of migrations, especially winter distribution. It is not known, for

instance, whether the walrus of Hudson Bay remain within the Bay during the winter or not, nor is it known which group of walrus visits Akpatok Island in early July each year. Something of the winter distribution could be discovered by air surveys, but the only final way of establishing migration habits is by marking the animals at the breeding grounds. This presents quite a problem, especially in species as large and formidable as the walrus, or as elusive as the beluga, and one of the most important problems to be solved is just how to mark them.

Systematic and zoogeographic studies

The fauna of the North American Arctic and Subarctic waters and coasts (except those of Greenland) is still poorly known. The large gaps in the distribution maps are being filled in, but even when the work of the *Calanus* and *Blue Dolphin* expeditions, and of the Point Barrow Laboratory, is published, there will still be a great deal of faunistic work to do, particularly in the central arctic section, and in the Beaufort Sea. The present signs are that when these gaps are filled in, the results will be very interesting. Ekman (1953, p. 159) has collected evidence to show that "a considerable part of the North Atlantic boreal fauna and the Polar Sea arctic fauna is derived from the North Pacific", and although the evidence is of the equivocal sort that zoogeography is often forced to use for lack of anything better, it is also the sort that is accepted by most zoogeographers. The shelf fauna of the North Pacific contains many more species and genera than are to be found on the North Atlantic shelf, and it is only in the Pacific region that endemic families are found. Given certain premises (which are not quite argument-proof), this is evidence for the dispersal of the fauna from the Pacific to the Atlantic. However that may be, there is good indication that there has been a dispersal from the North Pacific or Bering Sea area eastward to the Canadian Eastern Arctic, and also westward to the waters of the Siberian shelf, which has hitherto left the coasts of Greenland and of northwest Europe almost untouched. This is at present represented by the land-locked seal of Seal Lakes in the Ungava Peninsula, by certain of the fishes in Hudson Bay and Ungava Bay, and by several amphipod species; and the full study of the Eastern Arctic fauna will no doubt bring many more such examples to light. Such distributions are doubtless a legacy from early postglacial times, and the whole study of arctic zoogeography has an important bearing on the glacial and postglacial history of the North American Arctic.

Within the arctic zone, the phenomenon of circumpolarity appears to be fairly common, although the addition of the North American sector to the picture may well change our ideas in this as in other aspects of northern marine distribution. It may well be that there are variations within circumpolar species, which will be significant of isolation within the circumpolar area, especially in the littoral and benthonic species; and even for holoplanktonic forms there is the possibility of isolation by current systems. In the marine subarctic, the true monotypic circumpolar species is the exception

rather than the rule, and the investigation of the extent and quality of variation within subarctic genera is a matter of great interest to the student of evolution, and will be much extended by the filling in of the North American gap in our knowledge.

As for the fauna of the deep basins, there can be little doubt that even in the regions where most exploration has been made, as in the Greenland and Norwegian seas, there is still much to be added. In Baffin Bay our present knowledge is based almost entirely on the results of one short expedition, the *Godthaab* expedition of 1928. At the present stage of the study there appears to be a large number of species common to all the arctic basins (Arctic Ocean, Norwegian and Greenland seas, and Baffin Bay), a fact which may have interesting implications concerning the recent history of those depths. Before any firm conclusions can be drawn, however, there is much deep-water dredging and bottom sampling to be done.

There are many groups, which cannot be mentioned in detail here, whose systematics are in a somewhat chaotic state. For some of these, such as the Gadid and Liparid fishes, we need embryological studies in order to untangle the pattern of relationship, and for others, such as several amphipod families, we need large collections from the whole circumpolar field.

Finally, since zoogeography is a study of a dynamic, not a static, phenomenon, and since changes in the distribution of marine animals can be of decisive economic importance, it is necessary to keep routine observations going every year, or at regular intervals, not only upon the fauna itself, but upon the hydrographic conditions which, more than anything else, determine the composition of the fauna. Changes in the marine climate have not been treated in this paper, partly because of lack of space, partly because their existence and their overwhelming importance are now well established, and the continued study of them may be taken for granted.

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ON THE STATUS OF SOME ARCTIC MAMMALS

Robert Rausch*

THE mammal fauna of arctic Alaska is comprised of about thirty species, most of which are widely distributed. A few of these are essentially nearctic species, having extended their range northwestward during post-Pleistocene time. The majority, however, consists of forms which are either circumboreal in their distribution, or which have closely-related palearctic counterparts—considered specifically distinct by most North American mammalogists. Some of the foremost Old World workers, however, do not agree that Bering Strait constitutes a barrier which effectively separates the Old World fauna from the New.

North American mammalogists have not concerned themselves especially with the question of the distribution of boreal species, but rather have devoted themselves to the definition of local races. Some of the early investigators were aware of the strong tendency toward the circumpolar distribution of boreal species of mammals. Later workers, unfortunately, developed a remarkably restricted concept of mammalian speciation (e.g., Merriam's conclusions on species of the genus *Ursus*) which has seriously influenced the work of contemporary mammalogists.

In view of the recently intensified interest in arctic biology, with the attendant use of mammals by investigators working in diverse fields of research, it is more essential than ever to evaluate species relationships correctly. Such investigators cannot profitably maintain a provincial attitude toward speciation in North American mammals. To utilize pertinent literature concerning palearctic forms effectively, some of the nomenclatural complexities which obscure relationships must be eliminated.

The collection of Alaskan mammals has been essential to the investigations of the Animal-borne Disease Branch of the Arctic Health Research Center, at Anchorage, Alaska. Field work carried on for more than four years has resulted in the collection of approximately 4,500 mammals. The entire Territory has been covered, and considerable material has been obtained from regions where little or no work had previously been done. Since the survey phase of the work is nearly at an end, it seems desirable to summarize the information obtained.

Arctic mammals, mainly from the Brooks Range, have formed the basis for this paper, and each species is discussed in the light of holarctic distribution. Data on specimens from other parts of the Territory have been included whenever it would contribute to the clarification of the over-all distribution of a given species. An effort has also been made to synthesize the work of

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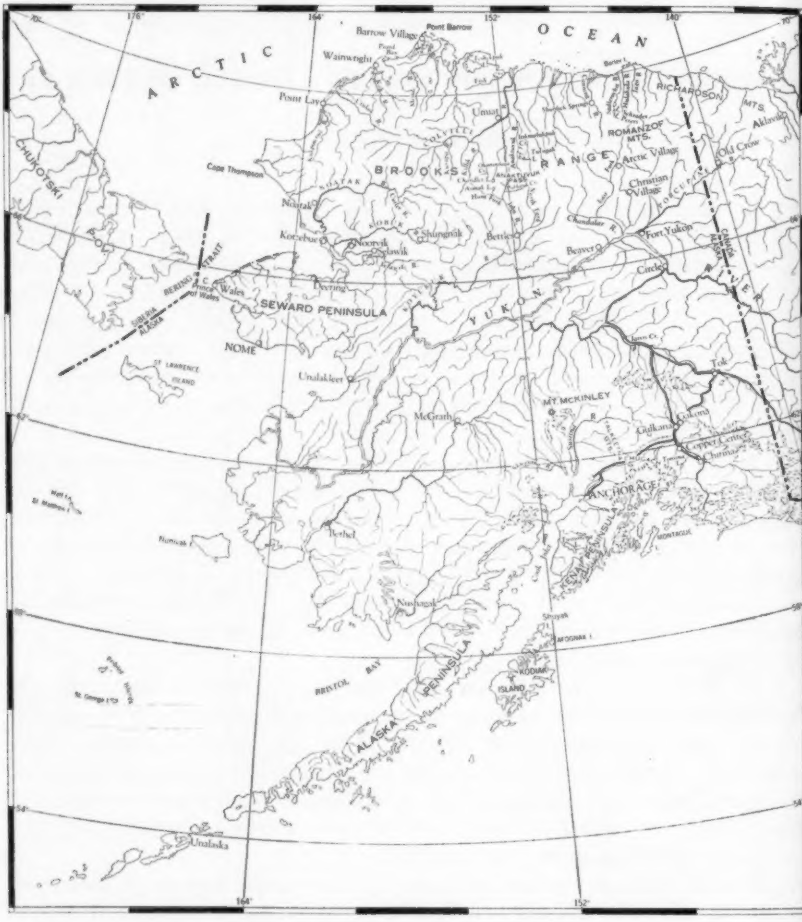

Fig. 1.

mammalogists who have concerned themselves with problems relating to the distribution of boreal mammals.

Some additional records from the Anaktuvuk Pass region, in the central Brooks Range, have been included to supplement those published earlier (Rausch, 1951). Particularly valuable material has been obtained from two localities in northeastern Alaska where little mammal collecting had previously been done. Because of the importance of the specimens collected, it seems appropriate to include here brief descriptions of these two areas.

Romanzof Mountains: The high, rugged mountains of the Brooks Range lying between the headwaters of the Sadlerochit and Jago rivers, and extending to within a few miles of the Arctic Ocean, are called the Romanzof Mountains.

The highest peaks of this group are more than 9,000 feet in altitude, and are snow-covered throughout the year. Two large lakes—Lakes Schrader and Peters—lie near these peaks, forty miles from the Arctic Coast, at an altitude of about 3,000 feet. Lake Peters, to the south, receives much glacier water and is consequently turbid. It is connected through a narrow channel to Lake Schrader, whose waters are clear. Lake Peters lies in a deep basin with steep walls to the east and west. The slopes along the western shore, however, are covered with willow (*Salix alaxensis* Cov.). Lake Schrader is surrounded by low rolling mountains covered with vegetation typical of dry alpine tundra. A large stream empties into this lake near its junction with Lake Peters, and extensive alluvial flats occur in this vicinity. These flats, as well as the stream banks, are grown to willow, and adjoin a marshy area at the south end of the lake. Polygonal formations are numerous in the marshy area, and the depressions support a dense growth of *Carex* spp. Sedge bogs are scattered along the lake and on the higher benches. Rock outcroppings are numerous on the ridges, and at the lower altitudes dwarf birch (*Betula nana* L.) is common. Water from the lakes drains off through a small stream at the north end of Lake Schrader, which flows into the Sadlerochit River a few miles north of the lakes. The steep valley of this stream supports the most luxuriant vegetation to be found in the region; for example, the willows are of exceptionally large size.

The Romanzof Mountain region has been described by Leffingwell (1919), and recent maps from air photographs have shown how accurate is his reconnaissance map of Lakes Schrader and Peters. His description of the area around the lakes is somewhat confusing at first glance as the names of the lakes have been transposed.

Arctic Village: Situated near the southern limits of the Brooks Range on the East Chandalar River, Arctic Village is about eighty-five miles south of Lakes Schrader and Peters. It is inhabited by Kutchin Indians, and its fluctuating population never exceeds 50 persons. Because of the isolated location of this village, the people depend for their livelihood upon hunting and fishing. The mountains here rise to about 6,000 feet. Lakes and ponds are numerous. The broad river valley is grown to spruce, and the taiga reaches its northernmost extent in Alaska in this region. The flora and fauna differ little from that of the southern timbered portions of the Brooks Range farther to the west.

Mammals

The species of mammals considered in this study are listed in systematic order. The specific names applied are correct insofar as I have been able to determine from a review of the literature and the study of comparative material.

Sorex obscurus obscurus Merriam. Dusky shrew.

The northernmost records of the dusky shrew are those of Rausch (1951), based on specimens from the north edge of the Brooks Range along the Anaktuvuk River. In northeastern Alaska I have not taken this species north of Beaver, on the Yukon River. No shrews of any kind were trapped in the

Romanzof Mountains. A small collection of shrews from Arctic Village was lost in transit, and no specimens of *S. obscurus* have since been taken here. Jackson (1928) recorded *S. obscurus* from a place twenty miles north of Circle, on the Yukon River. I have no knowledge of any other reports of its occurrence in arctic Alaska.

Sorex cinereus ugyunak Anderson and Rand. Arctic cinereous shrew.

Although I have not collected *S. cinereus* in northeastern Alaska, previously published records indicate that it occurs there. Anderson and Rand (1945a) reported it from the "Chandalar River, east Branch, south slope of Brooks Range," and from "Hulahula River, at northern foothills of Brooks Range." I recorded it from Anaktuvuk Pass and Umiat (Rausch, 1951). In the Canadian Arctic, it has been reported from the vicinity of Aklavik (Anderson and Rand, 1945a) and from other localities farther east (Banfield, 1951a).

A related form, *S. cinereus hollisteri* Jackson, has been reported from "the tundra near Wainwright" by Bailey and Hendee (1926). The eastern limits of the range of this form are unknown, but it is essentially a west Alaskan subspecies. Quay (1951) reported it from the Seward Peninsula.

Sorex cinereus is widely distributed in boreal North America, but much additional material will be required to determine the distribution of the various races.

Sorex tundrensis Merriam. Tundra saddle-backed shrew.

S. tundrensis was collected at Arctic Village only in northeastern Alaska, but it appears to be distributed over the entire Arctic Slope and the Brooks Range. Hall (1929) reported the species from Barrow, and at the same time stated: "The species ranges entirely across Alaska, from the Seward Peninsula to the mouth of the Mackenzie River." The tundra saddle-backed shrew was reported to be of widespread distribution in the central Brooks Range region (Rausch, 1951). Quay (1951) reported it from the Seward Peninsula, and 12 specimens were trapped at Nome in December 1952 by E. L. Schiller, of the Arctic Health Research Center. In northwestern Canada, Anderson (1946) reported it from the Mackenzie Delta region.

It is probable that *S. tundrensis* is conspecific with the obviously similar *S. arcticus* Kerr. The latter occurs farther east, and inhabits essentially the taiga of central Canada. Although Jackson (1928) indicated that their ranges are not contiguous, it is likely that such a conclusion has resulted through a lack of collecting in the Mackenzie–Arctic Red River region. In my opinion, the characters used to differentiate *S. tundrensis* from *S. arcticus* have subspecific, rather than specific, value. The literature regarding these two forms has been reviewed by Jackson (1928).

S. tundrensis is, moreover, closely related to the palearctic *S. araneus* L. Some of the earlier North American workers designated as *S. araneus* specimens later defined as *S. arcticus*. Regarding the affinities of *S. araneus*, Bobrinskiy *et al.* (1944) stated: "Very close forms (*S. tundrensis* and *S. arcticus*) are widespread from the western extremity of Alaska to central Canada." Chaworth-

Musters, cited by Ellermann and Morrison-Scott (1951), concluded that races of *S. tundrensis* occur in Siberia. Such an opinion was not expressed by Bobrinskiy *et al.* (1944). These workers, in fact, reduced the number of species of Russian shrews to but six.

Workers interested in the distribution of shrews in arctic regions can at least be aware that *S. araneus* is the palearctic counterpart of *S. tundrensis-arcticus*. Actual relationships, however, remain to be worked out on the basis of adequate comparative material and re-evaluation of morphological characters currently supposed to have specific significance. Some cranial details of these two species are shown in Fig. 2.

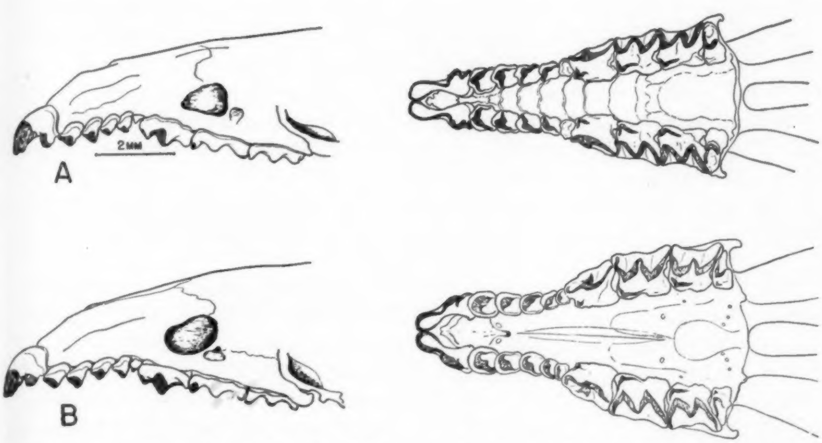

Fig. 2. Anterior portions of skulls of *Sorex tundrensis* (Alaska) (A) and *Sorex araneus* (Sweden) (B), showing dental and palatal characteristics.

Ursus arctos Linnaeus. Grizzly or brown bear.

Grizzly bears occur over all of arctic Alaska, but I have seen the largest numbers in the Brooks Range. Sign of bears was noted frequently in the Romanzof Mountains during the summer of 1951. A large dark brown adult, not collected, was observed feeding on the leaves of *Salix alaxensis* on the shore of Lake Peters. From the same general region, the skull of a specimen collected at Shublick Springs, in the valley of the Canning River, has been obtained (see Rausch, 1951). Farther south, the Indians of Arctic Village killed 8 of these bears during the summer of 1951. Of these, 4 specimens were secured for study. It is of interest that these Indians fear the bears, unlike the Eskimo farther to the west (Rausch, 1951), and will not attempt to kill them when hunting alone.

During the summer of 1952 the Nunamiut Eskimo killed a total of 7 bears in the vicinity of Anaktuvuk Pass. At least one additional animal was killed by poisoned baits disseminated by U.S. Fish and Wildlife Service predator

control men. The records I have for this region show that 36 bears were killed over a period of five years. The majority was male, indicating that male bears probably range more widely than the females. Reliable information on the home-range of grizzlies under natural conditions is not available. It is not known what effect, if any, hunting has upon the movement of such bears.

The specific status of North American grizzly bears is one of the most complex problems of mammalian taxonomy. The difficulty stems directly from the work of Merriam (1918), who concluded that there are 86 forms of grizzlies (and brown bears) in North America. He stated: "One of the unlooked-for results of the critical study of the American bears is the discovery that the big bears, like mice and other small mammals, split up into a large number of forms whose ranges in some cases overlap so that three or more species may be found in the same region" (p. 9). Such a view is not tenable, but evidence to the contrary is not easily secured.

The grizzly has been exterminated over much of its former North American range. Although it still exists in considerable numbers in Alaska, the problem of obtaining adequate material for study is nevertheless serious. The killing of bears for scientific purposes cannot often be justified, because of the rapid reduction of their numbers now being brought about through sport hunting. I have been fortunate, however, in securing 22 skulls, several with skins, from the central Brooks Range region. Full data on sex, date, and place of capture have been obtained. Additional specimens from various other localities within the Territory have also been assembled and pertinent material in various public and private collections has been studied.

From this material, I have concluded that a single, but highly variable, species of grizzly bear occurs in Alaska, and I shall endeavour in this paper to substantiate this conclusion. The extreme degree of individual variation demonstrated by the Brooks Range specimens is considered particularly significant.

In assigning specific names to various specimens of grizzlies which he obtained, Merriam failed to take into consideration any possibility of individual variation. Some "species" were named on the basis of a single skull, and in some cases not even the sex of the animal was known. Simpson (1945) has appropriately remarked that: "C. H. Merriam distinguished about 90 species of North American bears alone, but he had a (fortunately) unique conception of the character of a species, giving it less scope than most authors give a minor geographic race, not much more than an individual genetic family group. On such a system twin bear cubs could be of different species." (p. 225, footnote).

Further, Merriam's system of bear classification was based upon the hypothesis that the "species" of bears occurring in the same region maintain their identity by segregated breeding. In reference to this, Merriam (1918, p. 8) stated: "Some writers have advanced the view that the various species of bears freely interbreed. Let those so minded ask themselves the question, If promiscuous interbreeding were to take place, what would become of the species?". It would seem that Merriam concluded *a priori* that the species existed, and then went about finding means to support such a conclusion.

It is difficult to obtain much data on the breeding habits of bears. Most animals coming under close observation are usually seen over the sights of a rifle, and rarely live long enough to carry on their normal activities. Murie (1944) described the mating activities of two physically different male bears with a single female in the Mount McKinley region. Anyone working in a place where grizzlies still occur will soon note a lack of uniformity in the physical characteristics of the animals. Grizzlies, particularly males, travel considerable distances. This, together with their low density in most regions, suggests that breeding occurs on a chance basis alone. Under the stresses of breeding time it is most unlikely that bears are very selective in their matings, but rather that they must copulate according to opportunity. This is a fundamental concept which I adopt as valid. If one must wait until a large series of grizzlies, collected after having been observed *in coitu*, has been assembled, the problem is hopeless. If my conclusion that the grizzlies of Alaska represent but one species is valid, certain generalizations are possible.

It seems necessary first to consider separately the various characteristics used heretofore to differentiate species of grizzlies, in the light of a broader species concept.

External characteristics

Size: Grizzlies in Alaska vary greatly in size, even in the same locality. Over the Territory as a whole, the largest animals occur on Kodiak Island and the Alaska Peninsula. In other regions the adult bears vary in size between rather broad limits. In the Brooks Range, where I have made the most observations, the adult bears range from about 400 to 700 lbs., the latter weight though is rare. Such a size range appears to be characteristic of grizzlies over most of interior Alaska. Specimens from southeastern Alaska have not been considered in this study.

On Kodiak and Afognak islands, and on the Alaska Peninsula, the species attains its greatest size in North America. Extremely large animals are becoming scarce as a result of incessant hunting pressure, but specimens weighing from 1,200 to, perhaps, 1,500 lbs. are still killed occasionally. The maximum weight attained by these bears is not known, but the greatest reliable weight of which I know is 1,200 lbs. Weights exceeding 1,500 lbs. are frequently reported, but these are estimates and cannot be considered accurate.

The largest grizzlies in a given region are males, but some females exceed small males in size. There is rarely size-uniformity in a grizzly population. The majority of animals may be of about the same size, but unusually large and unusually small individuals are seen. Size depends in part upon age and condition. After full growth is attained, an individual bear varies in weight according to the season of the year, depending upon the amount of fat present. Very old animals, usually with broken and badly worn teeth, are often in poor condition, and in general have the lowest weights.

Measurements of external proportions of bears are so few that they have little or no value at present. Age, size, and sex all influence the various dimensions. Sport hunters regularly measure the length and width of the green hide.

I have made a few observations on these measurements, which confirm the obvious conclusion that they are worthless for scientific purposes, since they reflect only the enthusiasm and strength of the hunter and his guide.

It is noteworthy that maximum size in *Ursus arctos* is attained where an unlimited supply of high protein food is available. Thus, on Kodiak and Afognak islands, and, to a lesser degree, on the Alaska Peninsula, heavy salmon runs provide food during all of the warmer months when the bears are active. On Kodiak Island, the red salmon (*Oncorhynchus nerka* (Walbaum)) is available from late June to late September in the streams, and from late May at least until late November along the lake shores. Other species are abundant for shorter periods during the summer months. The same situation exists in Asia. In northeastern Siberia, particularly Kamchatka, great salmon runs occur. Here also *U. arctos beringianus* attains the largest size of any Eurasian form of *U. arctos*. For this form, Bobrinskiy *et al.* (1944) gave a maximum skull length of 445 mm. According to Johnson (1947) this bear attains a weight of 560 kg. in winter.

Colour: The colour of grizzlies is highly variable and, in my opinion, it has little or no taxonomic value. In the Brooks Range grizzlies range in colour from very pale (near Ridgway's Ivory Yellow,[1] but paler) to nearly black (near Blackish Brown). Some animals are entirely light-coloured, except for the legs and belly, but most have the buffy colour restricted to the head, shoulders and back. Despite the great range in colour, the general pattern is essentially the same: head and shoulders lighter, back and sides dark, belly dark, and legs and feet darkest. Even the very pale specimens have dark feet and legs, usually with a reddish tinge. It is true that the bears of a given region may be of predominantly one colour, but lighter or darker specimens are almost always observed. The bears of the Alaska Peninsula and Kodiak-Afognak may, in general, be more uniformly coloured, but on Kodiak Island I have examined specimens as light-coloured as any observed on the mainland, while others are very dark.

Claws: Grizzly claws are very variable in shape, size, and colour. Shape (curvature) and size depend mainly upon season of the year. Animals killed in the early spring usually have long, well-formed claws, but later they become badly worn through use. Extent of wear depends upon the terrain, rocky soils causing more rapid wear than others, particularly in places where bears frequently dig for rodents. When other food (e.g., salmon) is available, less wear results. Claw shape and size also appear to vary individually.

Claw colour varies from white to nearly black, and is related to some extent to the degree of pigmentation of the fur. Very pale-coloured bears in general have white or very light claws.

Internal characteristics

The skull: The differentiation of grizzly "species" has been based mainly on skull characters. Among these, skull size, relative proportions, and details of dentition have been considered important. Merriam (1918, p. 13) stated:

[1]Capitalized colour names are from Ridgway, R., 'Color standards and color nomenclature,' 1912.

"Cranial and dental characters among the big bears are very subtle. As a rule comparison of any two skulls of essentially the same size brings to light so many resemblances that one is likely to infer a far closer relationship than actually exists. This is because the big bears of the genus *Ursus* are such a closely interrelated group that the resemblances far outnumber the differences. Hence the greatest caution is necessary to avoid misleading conclusions."

The paucity of good series of bear skulls with complete data from any one region has in part prevented an evaluation of individual variation. However, even when good material has been available, the problem of variation has been little considered. Regarding the Alaska Peninsula bears, Merriam (1918, p. 125) stated: "Skulls of adult males which it seems necessary to call *gyas* present a surprisingly wide range in size and form. Among them are three quite different types which if isolated would undoubtedly develop into very distinct species." Merriam did not state why, in this case, he considered such "different types" to be conspecific. On the other hand, he considered *U. kidderi kidderi* Merriam, which has the same range as *U. gyas*, to be specifically distinct despite his statement: "Males of *kidderi* are sometimes hard to tell from females of *gyas*. . . (p. 107)". As far as I can determine, a single form, showing the usual variability, is found on the Alaska Peninsula. Its status is discussed in more detail below.

Bears occurring on Kodiak Island, hitherto known as *U. middendorffi* Merriam, are also quite variable. It is true that large adults show cranial characteristics which are relatively constant, but nevertheless some individuals differ strikingly from such "typical" specimens. I have examined a large series of skulls of this form, and Allen (1903b) studied 30 skulls of Kodiak bears and summarized their measurements. This form is likewise considered further below.

A small series of bears from the Alaska Range, designated as *Ursus toklat* Merriam, is in the collection of the U.S. National Museum. The skulls which I have examined have been relatively uniform, but show minor structural differences. The bears of the Mount McKinley region have been observed by several workers in the field, and nearly all of them have remarked on obvious physical differences.

The most significant bear material I have obtained consists of 22 skulls, with full collecting data, from arctic Alaska. These specimens, taken in the Brooks Range, exhibit unusual cranial variation. Some brief remarks on variation in Brooks Range bears were included in another paper (Rausch, 1951), under the species name *U. richardsoni* Swainson. Among these skulls, several adult male specimens differ conspicuously from one another, despite their having been killed in the same general region. Four specimens of unusual interest are shown in Fig. 3, and their measurements are given in Table I. All but one of these bears (orig. No. 9849; U.S. Nat. Mus. No. 293782) were killed in the Anaktuvuk Pass region of the central Brooks Range. They probably comprised interbreeding members of a single population. These animals, mature or aged males, were among 35 bears killed over a period of five years in the Anaktuvuk Pass region.

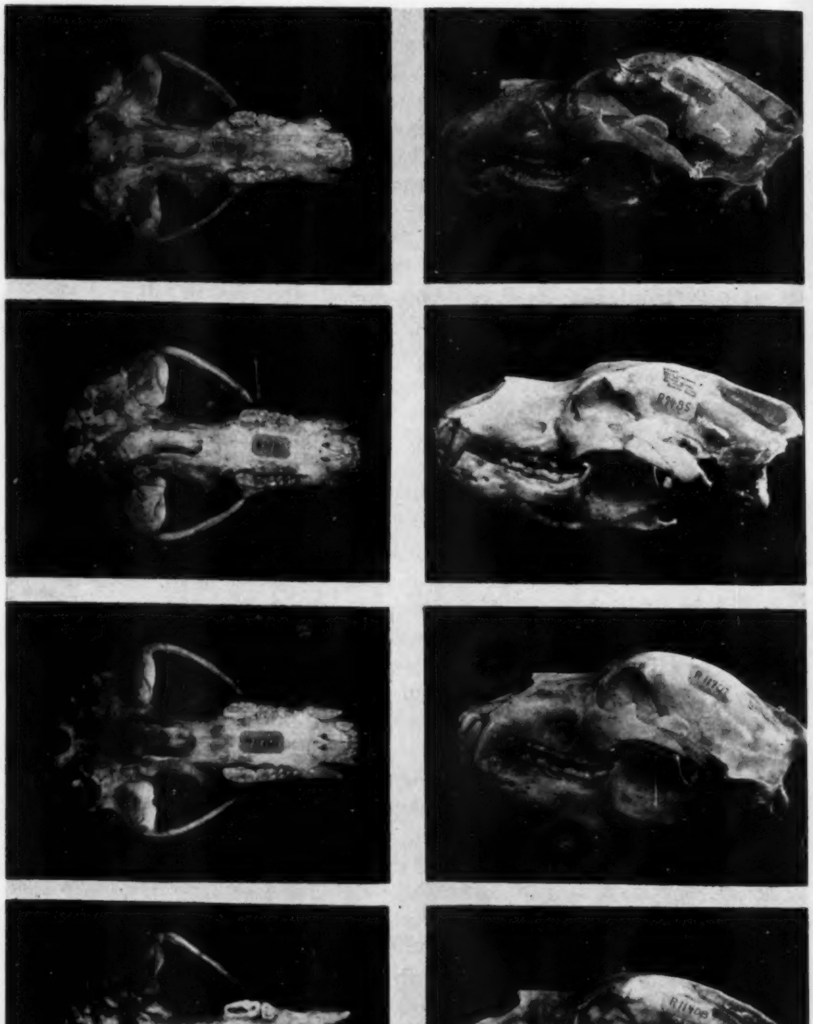

Fig. 3. Skulls of 4 specimens of Brooks Range grizzlies, all old or aged males, showing individual variation. Measurements are given in Table 1.

Table I. Cranial measurements of bear skulls illustrated in Figs. 3 to 6 (in millimetres).

No.	*Locality*	*Sex*	*Condylo-basal length*	*Zygo-matic width*	*Inter-orbital width*	*Palatal length*	*Post-palatal length*	*Upper tooth row length*	*Last upper molar length*	*Mastoid width*
Fig. 3										
R9849	Arctic Village	♂	358.6	236.8	87.0	185.0	166.5	140.2	35.2	186.0
R11707	Okominilaga Cr.	♂	335.5	218.3	83.3	173.8	155.8	128.6	37.8	155.7
R9485	Savioyok Cr.	♂	336.2	220.5	80.0	177.0	154.3	127.0	34.6	—
R11408	Upper John R.	♂	307.4	221.7	83.0	162.7	137.6	127.0	38.7	—
Fig. 4										
USNM 292125	Tulugak L.	?	199.0	119.0	48.1	104.5	88.3	—	—	84.2
R10533	Arctic Village	♂	236.3	131.8	53.1	124.8	108.0	108.0	37.4	95.1
R11588	Anaktuvuk Pass	♂	244.5	136.7	53.8	130.5	110.6	109.1	36.5	96.8
R11710	Inukpasukruk Cr.	♀	271.5	151.0	59.6	139.0	128.6	113.1	33.9	108.8
R12018	Inukpasukruk Cr.	♂	276.0	—	57.9	141.5	129.0	109.3	32.6	—
R12650	Anaktuvuk Pass	?	283.1	158.6	62.2	148.4	132.4	108.5	34.1	117.2
Fig. 5										
R11680	Cold Bay	♂	429.1	281.9	94.8	214.0	204.7	157.4	36.5	237.1
Fig. 6										
R12688	Olga Bay, Kodiak I.	♂	411.5	295.0	96.0	208.9	196.0	153.2	37.6	242.0

According to Merriam's system of bear classification, it would be acceptable to consider each of these 4 animals representative of a different species. I am convinced, however, that such is not the case. In another paper (Rausch, 1951, p. 165), it was stated, regarding the Alaskan distribution of *U. richardsoni*, that it "is widely distributed, and in Alaska its range appears to encompass at least the entire region north of the southern limits of the Brooks Range, including the Arctic Slope." It is necessary here to discuss also some of the species recorded from farther east, particularly in northern Canada.

In 1949 I studied pertinent bear material from arctic North America which has been deposited in various museums. Dr. R. M. Anderson kindly reviewed with me much of the material in the collections of the National Museum of Canada, among which were the type of *U. internationalis* Merriam, a large series of *U. richardsoni* which had been collected by Dr. Anderson, and a series of *U. macfarlani* Merriam. The study of this material and comparisons with Alaskan specimens led to the conclusion that all were conspecific. This was substantiated by the study of material in the U.S. National Museum, and in the American Museum of Natural History. Further work in Alaska has supported this conclusion.

As a result of the earlier work, it was concluded that a single species of bear extended across the entire North American Arctic. The variation observed in the Brooks Range bears has permitted a better concept of normal individual variation in grizzlies, and other Alaskan "species" may now be considered.

The comparison of my material with single specimens supposedly representing different species obviously had little value, since it was not possible to distinguish specific differences from individual differences. Where small series were available, as with *U. toklat* Merriam, from the Mount McKinley region, and *Ursus* sp. from Jarvis Creek, only small inconsistencies were sometimes noted. In light of observations made on the Brooks Range specimens, such differences cannot be considered significant. Moreover, the examination

of miscellaneous specimens from Alaska south of the Brooks Range has failed to disclose anything to support the concept that any of these differ specifically from the more northern specimens.

For the purposes of this paper, it seems impracticable to consider separate skulls in detail. There is apparently so much individual variation in bear skulls that generalizations regarding the animals of a given locality can rarely be made. A great range in skull size is to be expected. There may be considerable variation in the length/width ratio of the skull (condylo-basal length/zygomatic width) from a single locality. Skull profile is subject to much variation. In some cases the frontal region is gradually sloping and concave, while in others it is inflated and slopes abruptly. Rostral length is variable, and the nasals may show considerable range in length. The saggital crest may show much variation in degree of development, height, and antero-posterior extent. Variation is to be expected in the length and width of the palate. The ramus of the mandible varies greatly in form and relative length. The angle formed by the long axis of the skull with the horizontal, when the skull is at rest on a flat surface, differs from one individual to another largely on the basis of mandible shape. The maxillary tooth row shows considerable variation in length. The length of the last upper molar is highly variable. In the four skulls shown in Fig. 3, molar length ranged from 34.6 to 38.7 mm., and in a series of *U. toklat*, molar length ranged from 36 to 40 mm. A very large bear from the lower Alaska Peninsula had a molar length of only 36.4 mm., even though the condylo-basal length of the skull was 402 mm. Relative massiveness of dentition is highly variable. General massiveness of the skull, though related to age of the individual animals, is nevertheless subject to variation. Figure 4 demonstrates cranial changes associated with growth in *U. arctos*; the measurements for these specimens are included in Table I.

As a result of the study of Alaskan bears, I have no alternative but to conclude that a single, highly variable species occurs in the Territory. Excluding southeastern Alaska, 14 Alaskan species of grizzlies were recognized by Merriam (1918), as follows: (type locality indicated)

- *U. orgiloides* Merriam (Italio River)
- *U. alascensis* Merriam (Unalaklik River)
- *U. toklat* Merriam (head of Toklat River)
- *U. phæonyx* Merriam (Tanana Mountains)
- *U. internationalis* Merriam (Alaska–Yukon boundary)
- *U. kidderi kidderi* Merriam (head of Cook Inlet)
- *U. kidderi tundrensis* Merriam (Norton Sound)
- *U. eximius* Merriam (Knik Arm, Cook Inlet)
- *U. innuitus* Merriam (Seward Peninsula)
- *U. cressonus* Merriam (Wrangell Range)
- *U. alexandræ* Merriam (Kenai Peninsula)
- *U. gyas* Merriam (Alaska Peninsula)
- *U. middendorffi* Merriam (Kodiak Island)
- *U. kenaiensis* Merriam (Kenai Peninsula)

To this list should be added *U. richardsoni* Swainson, reported from Alaska by other writers.

Early investigators in North America, such as Richardson (1829) considered the grizzlies conspecific with the palearctic *U. arctos* Linnaeus. Acceptance of Merriam's concept would preclude consideration of this possi-

Fig. 4. Cranial changes associated with growth in *U. arctos*, from the Brooks Range. Probable ages are as follows, assuming January 1 as an average birth date (reading left to right from top): USNM292125 — 8 mos.; R10533 — 22 mos.; R11588 — 2 yrs. 4 mos.; R11710 — 2 yrs. 7 mos.; R12018 — 3 yrs. 8 mos.; R12650 — 4 yrs. 9 mos. All photographed at same scale. Cranial measurements are given in Table I.

bility by later North American mammalogists. A broader view of speciation in bears has been taken by certain Old World workers. For example, Bobrinskiy *et al.* (1944) included North America in the range of *U. arctos* as defined by them. Ellerman and Morrison-Scott (1951) stated, regarding the range of *U. arctos*, that it occurs "Also in North America."

If my conclusions regarding individual variation in grizzlies prove valid, the structural characters (cranial) which have been considered adequate to differentiate *U. arctos* also have lessened importance. I have, unfortunately, not found it possible to study many specimens of *U. arctos*. Ellerman and Morrison-Scott (1951) considered valid 7 Old World subspecies of this species.

Fig. 5. Skull of old male *U. arctos gyas*, killed near Cold Bay, Alaska Peninsula. Measurements are given in Table I.

Of these, I have examined skulls of only *U. a. arctos* Linnaeus, *U. a. isabellinus* Horsfeld, and *U. a. pruinosus* Blyth. Among these, a specimen of *U. a. pruinosus* from Tibet closely resembled some of the smaller Alaskan specimens. The range in size from the small *U. a. isabellinus* (India) to the great *U. a. beringianus* of northeast Siberia is greater than any size contrast of which I am aware in nearctic forms. J. A. Allen (1903b) compared skulls of *U. a. beringianus* with skulls of some North American bears. He stated: "Compared with skulls of *Ursus middendorffi* Merriam, from Kadiak Island, of corresponding age and sex, the breadth of the skull is much greater in proportion to its length, the anterior narial opening is much shorter, and the molars differ in relative size and form. It much more resembles in general contour and proportions the skull of the Barren Ground Bear (*Ursus richardsoni*), as perhaps should be expected." (pp. 164–5).

In my opinion there is no justification for considering North American grizzlies specifically distinct from *Ursus arctos*. It is necessary, however, to determine appropriate subspecific names in some cases.

Ursus horribilis Ord, 1815, appears to be the oldest available name for the grizzly. More conservative writers have recently used this name for all grizzlies, in view of the recognized unsuitability of Merriam's classification. Merriam obtained a topotype specimen which served for his characterization of this form (1918), but it is difficult to know how far the name *horribilis* can be applied. From Merriam's discussion, it is evident that he differentiated *horribilis* from forms he considered to be related on the basis of characters now known to be quite variable. In any event, the grizzly of the western

Fig. 6. Skull of old male *U. arctos middendorffi*, Kodiak Island. Measurements are given in Table I.

United States may be called *Ursus arctos horribilis* Ord. The fact that Merriam included animals from as far north as Yakutat Bay and Admiralty Island, Alaska, in his "*horribilis* group" would indicate that the subspecific name *horribilis* can be applied safely to the form formerly ranging over the western United States and western Canada. The members of Merriam's "*horribilis* group" were differentiated on the basis of minor cranial differences; since he had very few specimens of some "species"–in some cases only one–available for study, individual variation could not have been taken into consideration.

It is not certain whether the name *horribilis* can also be applied to grizzlies occurring farther north in Alaska and northern Canada. Richardson (1829) designated tentatively as *U. arctos americanus* the barren-ground bear "killed on the shores of the Arctic Sea" during Franklin's first expedition in 1821. The name *americanus* is preoccupied by *U. americanus* Pallas, 1780, and cannot be applied here. This bear was later given the name *U. richardsoni* Swainson. At present, it seems best to use the name *U. arctos horribilis* for the grizzlies of northern Canada and mainland Alaska.

Because of its unusually large size, and the relative uniformity of certain cranial characters, it seems appropriate to consider the Alaska Peninsula bear a distinct subspecies. It may be designated *U. arctos gyas* Merriam. A typical skull, large adult male, is shown in Fig. 5. Although variants occur, a large form is predominant. Merriam (1918) described some of the variants of this form.

The bear found on Kodiak, Afognak, and Shuyak islands also may be considered a distinct race. This form differs from the Peninsula bear in having

(in the adult male) a relatively great zygomatic width and a higher, more inflated cranium. Kodiak bears attain about the same maximum size as the Peninsula bears; however, breeding adults are not all of unusually large size. In June 1953 I weighed a breeding male which was killed while running with an adult female; this animal weighed 580 lbs. and measured 2123 mm. in total length. A female killed the same week, with yearling cubs, weighed only 375 lbs., with a total length of 1782 mm. These animals, of course, would have weighed considerably more in the fall of the year, since neither was fat.

This bear may be designated *U. arctos middendorffi* Merriam. A typical skull, adult male, is shown in Fig. 6.

In southern Alaska, large bears are occasionally killed which appear to be intergrades between the larger forms and the smaller bears of the mainland. These were considered specifically distinct by Merriam. Two of these from the Kenai Peninsula and Montague Island were designated as *U. kenaiensis* Merriam and *U. sheldoni* Merriam.

Some of the island species of southeastern Alaska have not been considered in this paper, mainly because I have not had adequate material for study. Merriam stated that the "species" of bears on islands often have their counterparts on the mainland of Alaska. On Admiralty Island, for example, Merriam concluded that five species exist together (*shirasi*, *mirabilis*, *insularis*, *neglectus*, and *eulophus*). He also listed five mainland species from which he considered the Admiralty Island forms to have been derived (*dalli*, *stikeenensis*, *tahltanicus*, *kwakiutl*, and *caurinus*). Merriam himself pointed out (1918) that the strait between Admiralty Island and the mainland is not more than five miles wide at the narrowest point. Grizzlies are powerful swimmers, and there can be little doubt that there has been a continual exchange of bears between the mainland and Admiralty Island, Merriam's island "species" being nothing more than individuals showing a normal (for bears) degree of variation. Although grizzlies show relatively great variation in cranial characters, the pattern of variation appears to be genetically restricted along certain definite lines. This may account for the fact that bears showing a given type of skull may occur almost anywhere within the range of the species. This situation might explain the "group" concept as defined by Merriam (1918). There is, however, a stronger tendency toward uniformity in some regions than in others. An interesting example of variation is shown by one of the Brooks Range specimens (Fig. 3, 11707), which resembles more closely a typical skull from Kodiak Island than it does any other Brooks Range specimens which I have seen. Conversely, skulls of some adult females and young males from Kodiak Island cannot be differentiated from skulls of bears from interior Alaska.

It is regrettable that predator control, excessive hunting, and the advances of civilization have exterminated the grizzly over the greater part of its original geographic range. Little can be learned of this interesting and important species in the United States and southern Canada except from early records (e.g., the journals of Lewis and Clark) and a few bones in museum collections.

A serious situation exists at present in Alaska, where the fishing interests and local cattlemen are attempting to bring about legislation which would

permit uncontrolled killing of the bears on Kodiak Island. These animals, subjected annually to a heavy legal hunting pressure, are killed at all times on the slightest pretext by the cattlemen. If present regulations were relaxed, the extinction of this unique animal would be certain.[1]

Ursus americanus Pallas. Black bear.

No further information has been obtained on the occurrence of the black bear in the Brooks Range. It is not found near Arctic Village, according to the Indians, but it is numerous near Christian Village, some forty-five miles to the south.

A large series of skulls from Alaskan black bears has been assembled, and it is evident that the species also shows much cranial variation. This work will be reported separately.

Vulpes vulpes alascensis Merriam. Alaska red fox.

Three red foxes were obtained in the vicinity of Arctic Village. None was seen in the Romanzof Mountains in 1951, and there was little sign of fox there. Skull measurements of 45 red foxes, the majority from the Brooks Range, are given in Table II.

Both Bobrinskiy *et al.* (1944) and Ellerman and Morrison-Scott (1951) (the latter on the authority of Pocock) regarded *V. vulpes* a species having circumpolar distribution. There does not appear to be any reason for disagreement with this concept, and the name *Vulpes vulpes* is consequently used here.

Alopex lagopus innuitus (Merriam). Continental arctic fox.

The irregular occurrence of this species in the Brooks Range has been reported (Rausch, 1951), and 2 specimens were obtained during the winter of 1951–2. A female arctic fox was trapped by Eskimo on 17 November 1951 on Itikmalukpuk Creek, northeast of Anaktuvuk Pass. According to cranial characteristics, this specimen was an adult. It weighed 2,800 grams. An adult male was killed on 9 March 1952, about six miles up the valley of the East Chandalar River, above Arctic Village. This was well within the taiga zone. According to the natives, the arctic fox is sometimes common around the head of the river.

Arctic foxes were abundant along the Arctic Coast during the winter of 1952–3, and large numbers were trapped by the Eskimo of Barrow and Wainwright. The brown lemming attained a high level of population density in the summer of 1952, and a fox abundance is an expected consequence.

Canis lupus ?tundrarum Miller. Wolf.

Wolves collected in northeastern Alaska are assigned to this form on the basis of locality. This is hardly satisfactory, but the study of available material has thrown some doubt on the validity of Alaskan subspecies of wolves as at present defined. It was evident, in comparing specimens of a large collection of wolf skulls, that considerable individual variation occurs.

[1]The firm stand taken by Clarence Rhode, Director, Alaska Division, U.S. Fish and Wildlife Service, has been effective in preventing unrestricted killing of bears on Kodiak Island.

Table II. Cranial measurements of 45 Alaskan red foxes (in millimetres).

Locality	*Sex*	*Condylo-basal length*	*Zygo-matic width*	*Squamosal constriction*	*Inter-orbital width*	*Palatal length*	*Post-palatal length*	*Maxillary tooth row length*
Anaktuvuk Pass	♀	138.5	74.5	48.3	26.7	71.7	66.0	64.9
Anaktuvuk Pass		137.3	73.9	47.7	25.7	70.4	65.7	64.4
Anaktuvuk Pass		144.6	74.6	48.3	28.0	75.8	68.0	69.2
Anaktuvuk Pass		132.8	74.1	46.8	27.7	70.3	61.9	62.3
Chandler L.		137.4	72.4	47.2	27.6	74.5	61.9	64.4
Chandler L.		132.8	75.3	46.9	27.4	68.1	63.1	63.3
Chandler L.		132.9	73.4	47.6	24.6	70.2	62.5	63.0
Okominilaga Cr.		133.5	73.3	47.3	28.8	68.5	64.3	63.9
Upper John R.		138.2	74.2	45.6	26.0	71.0	65.9	—
Noatak R.		138.6	76.2	48.1	27.6	71.5	65.3	65.1
Wainwright		139.5	76.0	48.4	30.2	71.4	66.6	67.4
Wainwright		142.0	77.9	48.2	31.8	73.7	67.1	68.8
Wainwright		134.7	75.0	46.8	27.0	70.6	60.7	64.9
Arctic Village		138.5	72.7	47.7	26.5	72.2	65.8	65.2
Arctic Village		141.7	78.8	47.6	27.3	73.4	66.2	66.5
Arctic Village		133.8	74.6	46.1	25.6	70.0	63.0	65.0
Fort Yukon area		140.0	78.1	48.3	30.1	75.0	63.3	65.8
Lake St. Ann		136.2	75.0	47.4	26.6	70.5	64.5	63.9
Copper Center		142.4	77.9	45.9	27.5	75.0	65.7	65.8
Tyone L.		142.1	78.8	47.5	26.5	75.1	66.7	67.5
Tyone L.		133.4	71.7	45.7	30.0	69.2	62.5	57.8
Tyone L.		130.2	71.1	46.2	26.1	68.7	60.6	60.5
Mi. 160, Glenn Hwy.		132.8	73.4	45.9	28.8	69.1	63.0	62.9
Mi. 170, Glenn Hwy.		135.3	72.6	46.5	25.7	70.2	64.1	65.5
Anaktuvuk Pass	♂	137.3	75.5	47.6	26.7	72.8	64.0	63.9
Anaktuvuk Pass		139.1	77.9	49.0	29.0	73.8	63.7	67.5
Anaktuvuk Pass		148.6	81.9	48.2	29.5	79.8	66.8	69.7
Anaktuvuk Pass		142.0	78.5	49.0	26.5	72.5	—	61.5
Asinak L.		140.9	76.0	47.7	28.2	75.3	65.5	67.1
Chandler L.		142.2	77.9	48.3	—	72.1	67.8	66.1
Chandler L.		137.1	76.3	47.8	27.8	67.9	67.0	64.5
Chandler L.		142.3	82.0	48.5	33.6	75.5	65.7	68.2
Chandler L.		140.1	77.4	49.1	29.7	72.4	65.7	65.7
Wainwright		145.7	77.1	47.8	28.2	75.5	68.2	69.6
Wainwright		143.8	79.9	49.8	28.7	74.9	67.3	68.0
Arctic Village		144.7	79.4	49.5	29.2	76.1	68.1	67.4
Arctic Village		138.3	78.2	47.5	29.3	73.6	63.2	65.4
Arctic Village		144.3	75.5	48.6	26.3	75.2	67.4	69.0
Arctic Village		138.4	69.5	46.0	24.7	73.6	63.2	65.9
Arctic Village		135.8	71.4	46.9	25.6	70.7	64.2	65.9
Arctic Village		146.1	79.8	47.9	28.3	77.4	67.5	68.7
Arctic Village		139.8	71.2	46.6	26.2	73.0	65.4	67.2
Copper Center		145.2	77.5	48.0	29.6	79.3	64.7	68.2
Tyone L.		155.5	90.8	52.4	33.2	83.6	70.5	71.7
Mi. 170, Glenn Hwy.		139.9	79.9	48.6	31.4	71.6	66.5	68.2
Average	♀♀	137.05	74.81	47.16	27.49	71.50	64.43	64.69
Average	♂♂	142.24	77.79	48.32	28.58	74.60	66.13	67.39

One wolf was collected near Lake Schrader and 4 specimens were obtained from the Indians at Arctic Village. During May 1952 I was able to collect an adult male a few miles south of Point Barrow—approximately at the type locality of *C. lupus tundrarum.* In addition, a large series of skulls, with full collecting data, is at hand from the central Brooks Range. From this region about 150 wolves have been autopsied, but it has not been possible to preserve all of them for mammalogical studies.

Skull measurements for 48 wolves are given in Table III. Most of these are arctic specimens, but a few others have been included for comparative

Table III. Cranial measurements of 48 Alaskan wolves[1] (in millimetres).

Date collected	*Locality*	*Age*	*Sex*	*Condylo-basal length*	*Zygo-matic width*	*Inter-orbital width*	*Palatal length*	*Post-palatal length*	*Squamosal constric-tion*	*Maxillary tooth row length*
Group 1										
Fall '51	Point Lay	approx. 6 mos.	♀	220.9	122.8	44.1	—	—	77.2	99.2
8/ 1/52	Itikmalukpuk Cr.	8 mos.		215.9	114.2	39.2	114.8	98.9	73.2	100.7
11/ 1/52	Anaktuvuk Pass	8 mos.		236.1	131.1	43.1	123.8	110.2	80.8	107.2
1/ 2/52	Chandler L.	9 mos.		221.8	124.3	39.4	118.4	102.4	75.2	100.8
6/ 2/52	Arctic Village	9 mos.		223.3	121.4	41.6	117.0	105.7	79.0	101.9
4/ 3/51	Anaktuvuk Pass	10 mos.		231.4	127.6	45.8	122.6	108.4	78.5	104.7
2/ 7/51	Lake Schrader	adult		—	135.0	46.0	—	—	—	107.0
21/ 4/51	Anaktuvuk Pass	adult		209.0	130.4	46.0	—	—	81.0	113.3
14/ 2/51	Anaktuvuk Pass	adult		232.6	133.9	49.6	119.5	111.5	78.6	106.3
Winter '51	Anaktuvuk Pass	adult		234.4	138.1	45.9	121.3	111.5	77.7	105.2
1951	Anaktuvuk Pass	adult		238.3	130.9	43.3	125.9	111.7	79.7	106.9
4/ 4/52	Ikiakpuk Cr.	adult		254.7	148.9	52.4	134.2	117.8	84.1	116.3
1/ 4/52	Anaktuvuk Pass	adult		256.5	133.3	42.0	137.5	117.9	79.9	118.3
4/ 4/51	Anaktuvuk Pass	adult		258.0	139.3	46.9	130.0	124.7	85.0	114.1
1/ 4/52	Anaktuvuk Pass	old adult		228.1	135.6	46.9	121.4	105.3	78.5	—
13/ 9/51	Arctic Village	old adult		229.3	137.0	48.4	120.5	107.8	81.6	103.4
4/ 2/52	Arctic Village	old adult		236.6	136.3	44.7	124.9	111.1	77.9	105.7
14/ 1/52	Anaktuvuk Pass	old adult		242.1	134.3	44.4	130.1	—	80.9	108.9
26/ 3/52	Tulugak L.	old adult		242.8	136.8	44.9	131.1	112.0	81.7	106.7
15/11/51	Anaktuvuk Pass	old adult		256.7	139.1	51.7	135.1	118.9	82.3	116.5
28/10/51	Tulugak L.	5 mos.	♂	237.6	125.3	41.7	125.8	109.8	81.4	107.6
19/12/51	Head, Hunt Fork	7 mos.		216.3	125.7	40.9	113.8	100.9	75.8	98.5
12/12/51	Killik R.	7 mos.		216.4	127.3	40.8	115.5	100.0	74.0	98.7
26/ 1/52	Anaktuvuk Pass	8 mos.		226.8	126.6	42.3	120.0	—	79.8	101.5
6/ 3/52	Anaktuvuk Pass	10 mos.		231.7	125.0	42.6	122.8	108.3	77.7	108.0
19/12/49	Ikiakpuk Cr.	adult		230.0	132.5	45.5	—	—	79.0	107.0
6/ 1/50	Anaktuvuk Pass	adult		227.0	123.0	44.0	—	—	77.5	99.5
16/3 /52	John R.	adult		237.1	132.2	45.9	128.9	108.0	77.3	108.3
4/ 4/51	Anaktuvuk Pass	adult		237.3	131.5	42.7	125.0	111.8	77.7	106.7
9/ 6/52	60 mi. S. Barrow	adult		241.8	144.6	47.1	130.0	110.7	81.8	109.7
Winter '52	Anaktuvuk Pass	adult		242.3	133.1	45.3	126.3	114.0	78.4	108.9
5/ 4/52	Anaktuvuk Pass	adult		242.7	133.8	49.5	126.5	114.9	78.7	111.3
3/ 4/51	Itikmalukpuk Cr.	adult		242.7	131.3	45.5	127.0	114.4	82.1	107.0
11/ 1/52	Chandler L.	old adult		233.7	124.0	42.5	121.4	110.8	78.4	105.5
Winter '52	Anaktuvuk Pass	old adult		239.4	149.7	48.6	122.7	114.5	84.0	—
1/ 2/52	Chandler L.	old adult		246.4	148.2	49.0	131.0	114.2	83.0	110.3
23/10/51	Anaktuvuk Pass	old adult		250.1	151.8	54.5	131.7	116.9	84.2	110.9
Dec. '51	Tulugak L.	old adult		253.5	148.8	52.9	131.1	119.3	81.3	—
6/ 3/52	Arctic Village	old adult		257.1	152.6	48.3	132.6	123.3	84.7	111.4
12/12/51	Anaktuvuk Pass	old adult		264.2	144.7	49.5	138.7	123.9	79.8	—
Group 2										
25/ 3/50	Tonsina L.	adult	♀	226.7	132.5	43.4	110.3	110.0	77.6	104.0
5/ 4/52	Clarence L.	adult		247.9	148.5	50.0	132.9	113.4	83.7	113.4
Feb. '50	Gulkana	old adult		237.6	135.8	46.1	126.0	109.8	77.4	106.5
Oct. '51	Venetie[2]	5 mos.	♂	224.2	113.9	38.7	116.9	103.2	75.4	—
Feb. '50	Gulkana	9 mos.		235.4	130.2	45.9	122.0	111.6	78.7	105.9
Mar. '51	Gulkana	adult		246.2	137.2	44.9	131.0	113.0	86.7	110.4
5/ 4/52	Clarence L.	adult		266.0	147.9	51.4	140.2	123.0	82.2	120.9
Group 3										
15/ 2/51	Tustumena L., Kenai Pen.	adult	♂	254.7	150.3	51.1	135.0	118.5	84.3	113.2

[1] These are separated, on basis of locality, into three groups, according to the commonly accepted subspecific designation: 1. *Canis lupus tundrarum;* 2. *C. l. pambasileus;* 3. *C. l. alces.*
[2] This animal was kept in captivity four months, and then died of canine distemper.

purposes. Age designations are given as accurately as possible. The age of young animals was computed by assuming a birth date of May 15. The date

of killing was known for all specimens. Comparisons of the skulls of young animals were also made with the skull of a captive male wolf which was five months old at the time of death (assuming the May 15 birth date).

Material from which *C. lupus tundrarum* was characterized (Miller, 1912) comprised specimens from widely separated localities. Young and Goldman (1944) summarized available data on North American wolves. Goldman prepared the taxonomic section, and had for study only 9 skulls of *C. lupus tundrarum*; of these, 5 were topotypes. Anderson (1943) studied 6 topotype specimens. *Canis lupus tundrarum* is differentiated as follows from forms with adjacent ranges (after Young and Goldman, 1944):

"Closely allied to *pambasileus* of Mount McKinley region, but color paler and grayer, the white less mixed with brown or buff on head, and back more sparingly overlaid with black; skull with heavier dentition. Similar also to *occidentalis* and *mackenzii* of Mackenzie in size, but color darker, the general dorsal area more extensively mixed with black, and the tendency toward pure white less evident than in *occidentalis*; dentition heavier." (p. 417).

The study of 40 skulls designated as *C. lupus tundrarum* (Table III) has made possible some understanding of normal variation. The largest skull I examined was but 4 mm. shorter in condylo-basal length than the largest specimen of *C. lupus pambasileus* recorded from Alaska by Young and Goldman. It exceeded in size the skulls of two adult *C. lupus alces* Goldman (1941), as well as that of an adult male of the same form in my possession. I do not recognize that *C. lupus tundrarum* can be differentiated from *C. lupus pambasileus* on the basis of heavier dentition. Brooks Range and Arctic Coast wolves exhibit a wide range of variation in tooth size. A few animals show very light, relatively small teeth, while a few have a dentition more massive than average.

I doubt that colour in Alaskan wolves has any taxonomic significance. There is a wide range in colour, from nearly white to almost black, but animals of either extreme and all intermediate colours may occur in any given region. Some wolves appear white from a distance, but all that I have seen close at hand have had some black-tipped hairs dorsally. The most nearly white specimen that I have seen, an adult male trapped by Eskimo near Anaktuvuk Pass, has been deposited in the collections of the U.S. National Museum (No. 294404). About half of all wolves killed or observed in the Brooks Range approach black in colour. Miller (1912) stated that the colour of *C. lupus tundrarum* is "said to be frequently white or whitish." It is likely, however, that he had some white specimens from the Canadian Arctic among the material he studied. Young and Goldman (1944) differentiated *C. lupus tundrarum* from *C. lupus occidentalis* Richardson and *C. lupus mackenzii* Anderson essentially on the basis of colour.

Restudy of the various subspecies of wolves seems necessary to determine whether the existence of so many named forms is justified. A series of each large enough to demonstrate normal individual variation is required. I doubt that *C. lupus tundrarum* can be differentiated from *C. lupus pambasileus*. The validity of *C. lupus alces* is also open to question. Wolves are very rare on

the Kenai Peninsula, and it might be expected that animals from farther north move into this region from time to time. In any event, clear-cut ranges cannot be established for subspecies of a mammal as capable of movement over great distances as is the wolf.

In order to obtain adequate material from Alaska and northern Canada it will be necessary to enlist the aid of local trappers. It is particularly regrettable that the great numbers of wolves killed by the predator-control activities of the U.S. Fish and Wildlife Service in Alaska are not being utilized for scientific purposes.

U.S. Fish and Wildlife Service methods for wolf control appear to be effective under arctic conditions. During the winter of 1951–2 wolves in northern Alaska attained a very high population density—quite possibly the highest ever observed for this region. The Eskimo of the Anaktuvuk Pass region killed 160 wolves by combined trapping and shooting. U.S. Fish and Wildlife Service predator control men killed over 200 in the same region of the Brooks Range and farther north on the Arctic Slope between Umiat and the mountains. Since much of the predator control activities centred in the hunting grounds of the Eskimo, the latter felt keenly the competition offered, and although they had killed a large number of wolves prior to the predator control activities, they killed none afterward.

Wolves are known to fluctuate greatly in numbers in arctic Alaska (see Rausch, 1951), and it seems questionable whether the high cost of wolf destruction would make a control program practicable even if it were considered biologically sound. It is of interest to the biologist that large numbers of ground squirrels, at least one grizzly, some caribou, and at least 9 sledge dogs succumbed to the effect of strychnine-poisoned baits used for wolf control in the Anaktuvuk Pass region. The question comes up whether this type of control might not result in a higher residual population of wolves, since the natural transmission of disease might be minimized in a population of already greatly lessened density. With the great wolf density of 1951–2 epizootic disease broke out which no doubt would have had violent effect on their numbers, had man not intervened with other controls. Rabies appeared among them, as was the case during the last time of high population density in 1944–5 (see Rausch, 1951). This was confirmed by rabies virus recovery[1] from the brain of a wolf killed while attacking tethered sledge dogs in an Eskimo camp. Rabies still occurred in foxes and dogs in eastern Alaska at the time of writing (December 1952).[2]

More serious was distemper, which broke out in epizootic proportions over all of arctic Alaska. Sledge dogs at Barrow, Wainwright, Point Lay, Anaktuvuk Pass, and in a camp along the lower John River, suffered greatly from this disease. About 500 dogs died at Barrow alone, and losses in other villages

[1]Rabies virus was recovered by the Virus and Rickettsia Section, Communicable Disease Center, Montgomery, Alabama.

[2]Foxes appear to be particularly important in the transmission of rabies. This is most obvious in highly developed regions (e.g., eastern and southeastern United States) where wolves no longer exist.

were of similar proportion. Arctic foxes died along the coast, and there is little doubt that the disease was disseminated through the wild canine populations from the coast to the dogs of the Inland Eskimo, and on southward. Since the wolves comprised a population highly susceptible to distemper, losses among them could be expected to be heavy. Distemper appeared in dogs in the Brooks Range in the spring and summer, after the predator-control program of early spring.

Martes americana actuosa (Osgood). Alaska marten.

In the previous work on Brooks Range mammals, it was remarked (Rausch, 1951) that the single marten collected differed rather strikingly in colour from specimens from other localities farther south. Two additional specimens from northeastern Alaska have been obtained, and these agree closely in colour with the animal collected to the west. These marten were trapped by Indians about thirty miles northeast of Arctic Village. Two skulls without skins were also obtained. Table IV compares measurements of Brooks Range martens with

Table IV. Cranial measurements of 17 Alaskan marten (in millimetres).

Locality	*Sex*	*Condylo-basal length*	*Zygo-matic-width*	*Inter-orbital width*	*Post-orbital width*	*Mastoid width*	*Palatal length*	*Post-palatal length*	*Maxillary tooth row length*
Arctic Village	♀	79.3	42.2	17.7	17.0	35.1	38.6	39.4	28.1
Arctic Village		78.4	40.8	16.5	17.2	34.4	39.0	38.6	28.1
Fort Yukon		81.4	47.0	18.5	15.5	36.8	39.8	39.8	29.4
Fort Yukon		—	43.7	16.6	16.5	35.4	38.7	—	28.5
Tyone L.		77.4	44.0	17.4	16.7	34.8	37.1	39.0	27.6
Mi. 160, Glenn Hwy.		75.5	42.0	16.4	17.2	34.8	37.1	37.3	27.1
Hunt Fork	♂	85.5	45.0	—	17.5	—	42.0	—	—
Arctic Village		83.6	51.3	19.0	15.2	38.9	40.5	41.9	29.6
Arctic Village		82.2	46.8	18.9	18.6	38.4	41.4	39.6	30.0
Fort Yukon		86.2	45.2	19.0	17.0	37.8	42.9	42.0	30.6
Fort Yukon		85.8	44.9	19.0	17.0	37.6	42.4	41.9	30.8
Fort Yukon		85.0	52.6	18.7	14.3	37.6	41.5	42.1	30.2
Tyone L.		84.7	53.1	20.0	16.6	39.0	41.3	41.8	30.5
Tyone L.		84.3	45.0	18.2	17.1	36.5	40.5	42.8	29.5
Tyone L.		83.5	44.9	18.0	17.2	37.2	41.7	40.6	30.2
Lake St. Ann		85.3	47.0	18.7	18.3	38.2	42.2	41.3	30.2
Skwentna		86.0	48.0	20.0	16.5	38.1	43.7	39.7	32.0
Average	♀♀	78.4	43.28	17.18	16.68	35.21	38.38	38.82	28.13
Average	♂♂	84.6	47.61	18.95	16.94	37.93	41.82	41.39	30.36

those from Fort Yukon (topotypes of *M. americana actuosa*) and farther south. No significant differences were recognized. Lampio (1951) found that the size of *Martes martes* L. in Finland increases northward, with maximum average size correlated with the lowest mean annual temperature. There is at present not enough available information to determine whether a similar situation exists in Alaska.

Preble (1908) discussed the characteristics of marten from the Mackenzie Delta region, and considered them identical with topotype specimens of *M. americana actuosa*. Coues (1877) has discussed the relationships of *M. americana* and related Eurasian species.

Mustela erminea arctica (Merriam). Ermine.

More than 60 ermine, most of them in winter pelage, have been obtained from various localities in the Brooks Range. The largest series came from the Anaktuvuk Pass region, but a large series was also secured at Arctic Village. I observed 3 ermine around a den along the shore of Lake Schrader during the summer of 1951, but did not take these specimens.

Since this weasel has recently been considered in detail by Hall (1951b), there is no need to include detailed measurements here. Large adult males from near Anaktuvuk Pass exceeded in average size the measurements given by Hall. Four specimens measured as follows: total length 340 mm. (319–353); tail length 83 mm. (82–90); hind foot length 49 mm. (46–53). A large male I collected on 31 May 1949, in the central Brooks Range, weighed 285.5 grams. Hall did not give any weight for an adult specimen.

After the study of pertinent Eurasian and North American material, Coues (1877) concluded that "The ermines of Europe, Asia, and America are specifically identical." The work of later investigators has substantiated Coues's conclusion. *M. erminea arctica* of Alaska and arctic Canada occurs also on Kamchatka, according to Ognev (1935), Bobrinskiy *et al.* (1944), and Ellerman and Morrison-Scott (1951). Hall (1944), on the basis of 9 skulls, differentiated the Kamchatka form as *M. erminea digna* Hall, 1944, and maintained this opinion in his recent review (1951b). It is clear that the Kamchatka form is closely related to *M. erminea arctica*, but additional work, based on an adequate series of specimens, seems necessary to determine their relationship.

Mustela rixosa eskimo (Stone). Least weasel.

A single subspecies of least weasel, *M. rixosa eskimo*, occurs in Alaska according to Hall (1951b). Four Brooks Range specimens were identified earlier as *M. rixosa rixosa* (Bangs) (see Rausch, 1951). There seems to be no reason to question Hall's conclusion, although he had no Brooks Range specimens for comparative study. Nevertheless, the few specimens I have do not show the broader, larger skull of *M. rixosa eskimo*; they also average smaller in external measurements. Such characteristics are in part correlated with age.

Little additional information has been obtained on this species in arctic Alaska. I have heard from the Eskimo that it sometimes becomes common along the Arctic Coast during times of high density of *Microtus* populations, but I have not observed this. No specimens were obtained in northeastern Alaska.

Allen (1903b) apparently was the first to point out that *M. rixosa* is a circumpolar species. He differentiated it from *M. nivalis* Linnaeus on the basis of external characters, including size. However, Bobrinskiy *et al.* (1944) and Ellerman and Morrison-Scott (1951) regarded *M. rixosa* as a synonym of *M. nivalis*. Hall (1951b) did not agree with this concept. Further work is needed to establish whether *M. nivalis* occurs in North America, or whether the Siberian races now attributed to it are actually subspecies of *M. rixosa*. It seems expedient to adopt Hall's concept for the present time, although it is possible that it is too restricted.

Mustela vison Schreber. Mink.

Although it was reported that mink occasionally occur in the Brooks Range (Rausch, 1951), no additional information has been obtained. I have secured a good series of mink from the vicinity of Fort Yukon, but have no specimens from farther north. The Arctic Village people know nothing of the occurrence of the mink in the eastern Brooks Range.

Lutra canadensis (Schreber). Otter.

Otter are frequently trapped about thirty miles south of Arctic Village, but the Indians have no knowledge of its occurrence in the mountains. It is apparently uncommon so far north, even though the taiga extends much farther in this region.

Gulo gulo luscus (Linnaeus). Wolverine.

A single wolverine, not collected, was observed near Lake Schrader in the Romanzof Mountains. Seven specimens were obtained near Arctic Village, 2 having been trapped some twenty-five miles to the east. Skull measurements and other data for a large series of Alaskan wolverine are given in Table V. Many of these specimens were collected in the Brooks Range.

Coues (1877, p. 43) in reference to the wolverine, stated: "The identity of the animals of the two continents is to be considered fairly established, whatever range of variation in size and color either may present." The work of Degerbøl and Freuchen (1935), who also concluded that the North American and Eurasian wolverines are conspecific, was briefly discussed in another paper (Rausch, 1951). Bobrinskiy *et al.* (1944), with whom Ellerman and Morrison-Scott (1951) agreed, considered the wolverine a species having circumpolar distribution.

I have been able to obtain for study but a single skull of *Gulo gulo*, from the upper Lyapin river, northern Ural Mountains. Comparisons with a series of 41 skulls of Alaskan wolverine now in my possession has disclosed no appreciable differences. The work of Degerbøl and Freuchen was particularly thorough, however. It is evident that the species is highly variable in regard to skull characters. I agree with the above-mentioned workers that the name *Gulo luscus* should be considered a synonym of *Gulo gulo* Linnaeus.

In 1905 Elliot described *Gulo hylaeus* from the upper Susitna River, Mount McKinley region of Alaska. Through the courtesy of Colin C. Sanborn, Curator of Mammals, Chicago Natural History Museum, I have available for study 4 topotype specimens. This species was differentiated on the basis of presumed colour differences, and minor cranial differences (relatively narrow skull with unusually large auditory bullae). The study of all material indicated that the skull differences fall within the range of normal variation. Colour in North American wolverine, at least in Alaska, has no specific value. I have seen striking variation in the colour of Alaskan animals from the same locality, as mentioned earlier (Rausch, 1951). I conclude, therefore, that *Gulo hylaeus* Elliott, 1905, is a synonym of *Gulo gulo luscus* Linnaeus.

The measurements of 4 of Elliot's specimens are included in Table V. Data on reproduction and certain growth changes in the wolverine will be

Table V. Cranial measurements of 41 Alaskan wolverine (in millimetres).

Locality	*Date*	*Sex*	*Condylo-basal length*	*Zygo-matic width*	*Squamosal constriction*	*Inter-orbital width*	*Palatal length*	*Maxillary tooth row length*
Anaktuvuk Pass	10/ 1/51	♀	133.0	94.5	72.0	39.0	—	49.0
Hunt Fork	7/ 2/51		133.3	89.8	67.3	—	69.8	48.8
Arctic Village	11/ 1/51		132.3	97.6	72.0	39.4	68.0	49.0
Arctic Village	21/ 3/52		138.0	97.0	—	39.0	69.0	—
Mi. 31, Tok Rd.	Jan. '50		139.3	99.6	70.8	38.5	72.5	53.0
Mi. 170, Glenn Hwy.	25/ 1/50		133.0	93.0	69.0	36.5	69.0	50.3
Chitina	Jan. '50		129.0	90.5	68.6	37.1	65.6	46.6
Skwentna	12/ 2/53		138.7	99.2	75.0	39.4	71.7	52.7
Skwentna	26/ 1/53		134.8	96.5	73.7	36.0	69.9	49.8
Skwentna	25/ 1/53		134.8	95.2	70.7	36.5	69.1	50.6
Anaktuvuk Pass	17/12/48	♂	144.5	103.4	80.7	42.6	—	51.5
Anaktuvuk Pass	Winter '48		147.5	107.5	76.1	42.5	—	54.9
Anaktuvuk Pass	Feb. '50		145.0	106.5	71.4	40.0	76.2	53.4
Anaktuvuk Pass	Feb. '50		143.5	103.0	75.3	38.2	75.4	54.6
Anaktuvuk Pass	28/ 2/52		151.2	109.6	83.5	44.5	76.6	52.5
Anaktuvuk Pass	25/ 3/52		151.7	107.0	83.0	44.0	76.9	54.6
Anaktuvuk Pass	4/ 4/52		138.6	108.2	81.9	46.7	69.1	50.3
Upper John R.	Winter '48		141.6	101.0	78.0	38.6	—	51.9
Upper John R.	3/ 1/49		140.7	101.2	77.0	38.6	—	51.3
Upper John R	7/ 3/49		143.7	105.1	80.6	43.4	—	52.0
Head, John R.	19/ 1/52		144.8	105.6	81.9	40.6	76.3	51.6
Head, John R.	21/ 2/52		143.0	103.3	80.0	39.5	73.0	54.7
Upper Hunt Fork	10/12/51		144.0	107.0	78.4	40.5	—	51.5
Kalutagiak Cr.	9/ 2/51		137.2	105.0	77.5	41.5	72.6	52.0
Arctic Village	28/10/51		143.4	104.2	—	40.5	74.3	54.6
Arctic Village	1/11/51		148.0	101.6	76.6	40.3	75.0	55.2
Arctic Village	28/ 2/52		144.0	100.5	76.7	39.4	75.5	53.0
Arctic Village	1/11/51		142.4	102.5	76.8	40.5	72.5	52.1
Arctic Village	6/ 1/52		143.6	108.1	83.2	39.5	74.5	53.8
Arctic Village	1/11/51		150.5	108.4	82.2	42.8	78.7	55.7
Snake R., 17 mi. Nome	11/12/52		145.5	99.9	75.9	39.7	72.7	53.3
Mi. 31, Tok Rd.	Jan. '50		--	111.8	—	40.8	78.2	55.0
Mi. 180, Glenn Hwy.	Apr. '51		149.0	103.1	75.9	43.0	78.8	55.6
Skwentna	25/ 1/53		152.8	105.1	—	40.5	78.6	55.5
Talkeetna Mts.	27/12/51		—	105.3	79.5	40.0	78.0	54.4
Talkeetna Mts.[1]	22/ 7/52		143.8	95.0	72.4	38.8	71.8	—
Susitna Valley[2]	4/ 2/53		—	—	—	—	—	—
Average		♀ ♀	134.62	95.29	71.01	37.93	69.40	49.97
Average		♂ ♂	145.0	104.57	78.45	41.03	75.23	53.40
Gulo "hylaeus" — topotype specimens								
Susitna R.	1904	♀ ?	140.3	99.4	73.9	39.0	72.2	52.2
Susitna R.	1902	♂	150.5	113.2	82.4	40.3	79.4	52.8
Susitna R.	1904		148.9	110.8	77.1	41.3	78.5	55.6
Susitna R.	1904		143.9	100.0	74.5	39.8	76.7	55.0

[1] Immature animal; permanent dentition incomplete; weight 8,618 grams.
[2] Largest Alaskan specimen examined; weight 17,480 grams; TL 1000; T 210; HF 192 mm.

presented in another paper (Wright and Rausch, 1953).

A bill providing for a bounty on wolverine in Alaska was introduced in the Territorial Legislature in early 1953. Wolverine are never numerous, and enactment of such a law would cause them to be subjected to greater persecution than is the case under their present status (now may be killed at any time). It also would contribute additional support to the few who hunt animals by aircraft for the bounty, and provide opportunity for the illegal killing of bears and other large animals under the guise of hunting for wolves and wolverine. Wolverine fur is important in the economy of Alaskan Eskimo. There is,

moreover, no biological knowledge which would support the bounty system insofar as the wolverine is concerned.[1]

Felis lynx canadensis Kerr. Canada lynx.

No information was obtained on the occurrence of the lynx in northeastern Alaska. Hares are on the increase, and it may be expected that lynx will become more numerous in the next few years. It is known that lynx may travel far north of the taiga zone following the decline of the hares. A lynx was obtained from Eskimo who trapped it at the mouth of Publatuk Creek in early 1953. This species was not numerous in the central Brooks Range in 1952–3.

After consideration of all pertinent material, Ellerman and Morrison-Scott (1951) concluded that there is no justification for splitting the cats into several genera. Moreover, they concluded that *Felis lynx* is a circumpolar species. Their nomenclature is accepted here. Bobrinskiy *et al.* (1944) came to the same conclusion earlier. The latter writers also stated that *Felis lynx* occurs in the "forested regions of North America."

Lepus americanus dalli Merriam. Snowshoe hare.

A large series of snowshoe hares, in winter pelage only, was obtained at Arctic Village. Since Arctic Village is perhaps in the zone of intergradation between *L. americanus dalli* and *L. americanus macfarlani* Merriam, the specimens are assigned to the former with some reservations. No further information was obtained on the status of this hare in arctic Alaska.

Lepus timidus othus Merriam. Arctic hare.

The arctic hare has been rare in northern Alaska for at least five years. The occurrence of this species in arctic Alaska was discussed previously (Rausch, 1951). Hall (1951a), in his synopsis of North American Lagamorpha, pointed out that general comparisons indicate that *Lepus othus* is conspecific with the palearctic *L. timidus* Linnaeus. Ellerman and Morrison-Scott (1951) stated that *L. timidus* occurs "Probably in North America." Bobrinskiy *et al.* (1944) stated that *L. timidus* occurs in North America. Hall did not make the indicated nomenclature change, but it seems justified on the basis of existing evidence.

An adult male of this species was recently obtained near Wales, on the Seward Peninsula, by E. L. Schiller, of the Arctic Health Research Center. Quay (1951) secured no specimens on the Seward Peninsula, and these hares were known to be rare there during 1947–8.

Marmota marmota broweri Hall and Gilmore. Arctic hoary marmot.

One specimen of this marmot was obtained at Arctic Village, where the species is common. None was observed in the Romanzof Mountains, although it is probable that it occurs there. Twenty-seven of these marmots have been obtained, most of which were collected from the Anaktuvuk Pass region.

[1]As of 1 July 1953 a bounty of $15.00 each will be paid on wolverine by the Territory of Alaska.

M. caligata broweri (=*M. marmota broweri*) was described by Hall and Gilmore (1934) on the basis of 4 specimens which were received from Charles Brower, of Barrow. Brower had in turn obtained the specimens from Eskimo living at Cape Thompson and Point Lay. To anyone familiar with the topography of western Alaska, it is obvious that suitable marmot habitat cannot exist in the vicinity of these villages, both of which lie on the Arctic Coast, at the edge of the coastal plain. I have attempted to obtain information through talking with old Utukamiut, or Kukmiut, Eskimo who formerly inhabited inland country around the head of the Utukok River. These people, now living in coastal settlements, still hunt far inland, and from their youth have been familiar with the region around the west end of the Brooks Range. The Point Lay people have regularly travelled up the Kukpowruk River to hunt in the mountains, and the country around the head of this river is the nearest possible marmot habitat. Consequently, the probable type locality for *M. m. broweri* is near the head of the Kukpowruk River, at about lat. 69°N.

The specific status of marmots designated as *M. caligata* (Eschscholtz) has been open to question for several years, as discussed by Ognev (1947). Wehrli (1935) considered the black-capped marmot of Kamchatka to be identical with the nearctic *M. pruinosa* Gmelin (=*M. caligata* (Eschscholtz)). Bichner (1888, cited by Ognev, 1947) concluded that *Arctomys caligata* Eschscholtz= *A. baibac* var. *camtschatica* Pallas=*A. camtschaticus* Brandt. In regard to this problem, Ognev (1947) stated: "The Kamchatka marmots, unquestionably, are close to the Yakutsk and Transbaykal forms. All of these represent subspecies with respect to their systematic characteristics, and gradually grade one into the other." He stated further: "At the present time it is difficult to divine with sufficient certainty the centre of colonization of the east-Siberian mountain marmots of the group *camtschatica*, because of the lack of study of the systematic interrelationships of these marmots with *M. caligata* Eschscholtz." Also, "It is extremely probable that *camtschatica* and *caligata* are related, perhaps even one and the same thing and have common ancestors. . .".

This problem was not considered by Bobrinskiy *et al.* (1944). Ellerman and Morrison-Scott (1951) listed *M. camtschatica* as a subspecies of *M. marmota* Linnaeus, 1758. These writers defined the distribution of *M. marmota* in Siberia to be ". . . Kamchatka, region of Lake Baikal and Verhoiansk Mountains, in Eastern Siberia, north-eastwards to Anadyr region," and stated that it occurs "Also probably in North America."

Although a large amount of Eurasian material is difficult to obtain in North America, I have assembled an adequate collection of marmot skulls for study. These included series of all North American species of marmots, with the exception of *M. vancouverensis* Swarth, and two of the three Eurasian species (excepting *M. caudata* Jacquemont) from various localities in Europe and Asia. Unfortunately I have not secured any specimens of *M. marmota camtschatica*, the form probably resembling most closely the North American *M. caligata*. As a result of this work, I have concluded that *M. caligata* is conspecific with *M. marmota*.

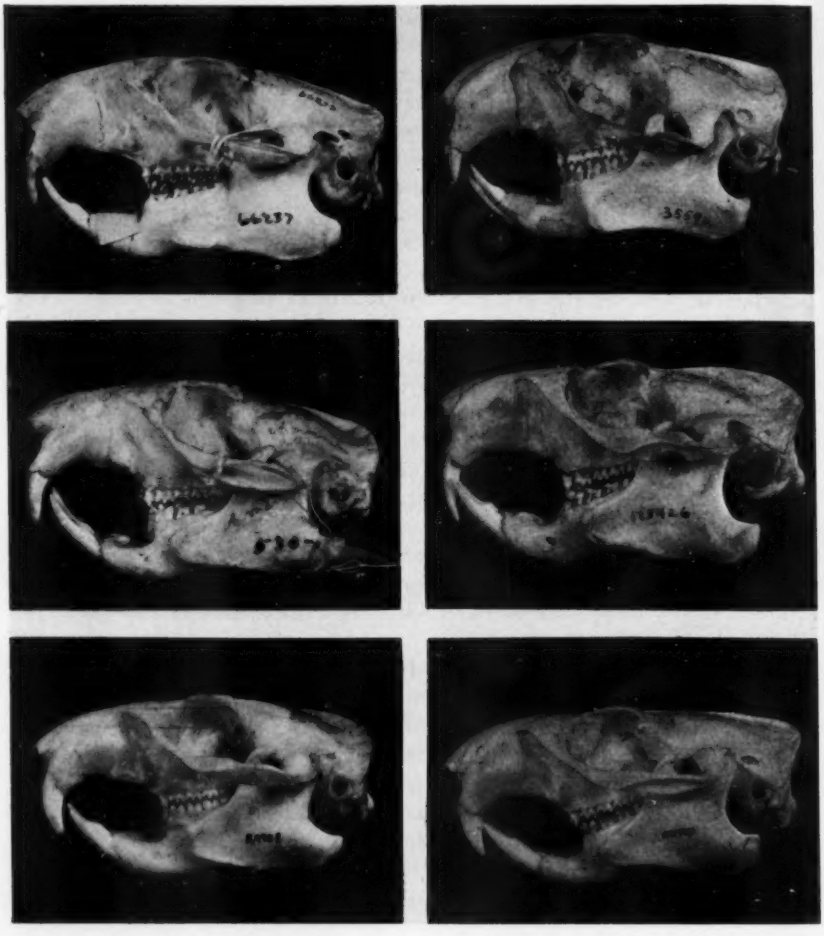

Fig. 7. Skulls of five subspecies of *Marmota marmota* (reading left to right from top); *M. m. marmota* L. — 66237, Bavarian Alps; *M. m. marmota* — 35593, Switzerland; *M. marmota* ssp. — 5307, south Russia; *M. m. baibacina* Brandt — 175426, Altai; *M. m. broweri* Hall and Gilmore — R9932, Brooks Range; *M. m. caligata* Eschscholtz — R11701, southern Alaska.

On the basis of the skulls at hand, it is evident that each form grades into the next, demonstrating a cline which extends from Switzerland and south Germany across Siberia into North America. The European specimens (*M. m. marmota* Linnaeus) are characterized by a heavy rostrum and strongly arched nasals. Progressing eastward there is a gradual flattening of the dorsal line until the profile is similar to that of North American specimens. This flatness of profile reaches its extreme, in specimens available here, in *M. marmota baibacina* Brandt, of the Altai. In other cranial details, likewise, closer agree-

ment with North American forms is seen farther to the east. Considerable variation in cranial details is evident in *M. marmota* as a whole. Differences may be seen especially in shape of nasals, relative position of fusion-point of temporal ridges, degree of concavity of frontal region, relative size of bullae, shape of parietal bones, degree of concavity and other details of palate, and in mandible shape. Such differences, however, are relatively slight and have only subspecific value. Skulls of representative forms are shown in Fig. 7.

M. marmota broweri differs from the three palearctic subspecies in the following: Nasals narrower, as above. Rostrum lighter, and much less curved than in *M. marmota marmota.* Zygomata more flaring, and zygomatic processes of the maxillae are relatively much smaller. The angular process of the mandible is relatively smaller. In relation to *M. marmota baibacina,* the squamous temporal bones are narrower dorsally and more deeply indented behind the zygomatic processes. *M. marmota broweri* resembles the palearctic forms in size of bullae.

M. marmota broweri differs rather strikingly from *M. marmota caligata,* which has an extensive geographic range in Alaska. The rostrum of *M. marmota broweri* is narrower and less massive. The nasals are narrower and taper backward, the least width being about ⅔ of their length from the anterior ends. The zygomatic processes of the maxillae are very narrow dorsally, where they join the frontal bones and premaxillae; this results in a more abrupt flaring of the zygomata. The zygomatic width is relatively greater in my specimens, although Hall and Gilmore (1934) concluded that the opposite was true. The postorbital processes are more abruptly flaring. The mastoid width is relatively less, and the bullae are larger. The mandible is straighter and the angular process is relatively smaller.

M. marmota broweri also differs from *M. marmota caligata* in external appearance, although the colour pattern is essentially typical of the group. It differs from all other races of *M. marmota* that I have seen in the uniform black colouring of the face. This feature alone distinguishes it readily from related forms. The pelage of this marmot is very dense, and the hairs relatively fine—differing in this respect from the related North American forms. The individual hairs are tricoloured: black in the proximal half, then grey distally, with a darker tip. The ground colour is consequently grey, nearest to Pale Smoke Gray. The amount of black is variable, but heaviest dorsally along the midline. There is usually a solid black area covering the third quarter of the body dorsally. This area may be brownish on some specimens, resembling Chaetura Black. The rump area, roughly the last body-fourth, ranges in colour from something darker than Prout's Brown to Warm Buff. The heavily-furred tail is variegated, a combination of dark brown and Cinnamon-Brown. The belly, throat, legs, and feet are essentially dark grey. The feet are not as lightly coloured in my specimen as Hall and Gilmore's description (1934) implies.

The Brooks Range marmot has a valuable fur. The average price for a good adult raw skin is $6.00. The Eskimo find a ready market for the animals they trap.

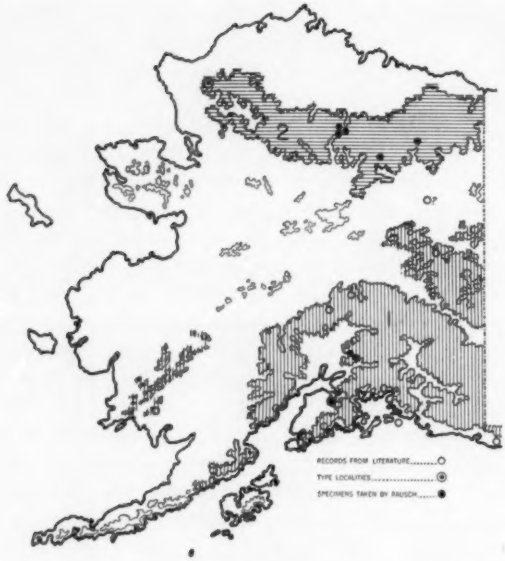

Fig. 8. Distribution of *M. marmota caligata* (1) and *M. marmota broweri* (2) in Alaska. For all distribution maps, mountain ranges are shown, based on the 2,000-foot contour lines.

As a consequence of the broader view taken here of the species, the status of two isolated forms becomes especially interesting. Both *M. olympus* (Merriam) and *M. vancouverensis* Swarth have been considered well differentiated members of the *caligata* group. As far as I can determine from the study of adequate material, I see no reason to maintain *M. olympus* as a full species. It is not as atypical as *M. marmota broweri*, for example. The fact of its isolated geographic position does not in itself justify specific rank. It should, in my opinion, be considered a subspecies of *M. marmota.* The situation is probably identical for *M. vancouverensis.* I have not, however, had any material of this form. According to the views set forth here, the names of North American hoary or black-capped marmots should be:

M. marmota caligata (Eschscholtz)
M. m. cascadensis Howell
M. m. nivaria Howell
M. m. okanagana (King)
M. m. oxytona Hollister
M. m. raceyi Anderson
M. m. sheldoni Howell
M. m. vigilis Heller
M. ?m. broweri Hall and Gilmore
M. m. olympus (Merriam)
M. ?m. vancouverensis Swarth

An up-to-date and more accurate distribution map of marmots in Alaska has been prepared (Fig. 8). This is based on records cited by Howell (1915) and others, and on my material. It is possible that *M. m. broweri* intergrades southwest of the Mackenzie Delta with *M. m. caligata.* Porsild (1945) tentatively assigned to *M. caligata caligata* marmots known to occur west of the Mackenzie Delta and southwest of Aklavik. No specimens were obtained.

If future investigations show the concept of marmot speciation presented herein to be untenable, it would seem to me that *M. m. broweri* would have to be considered a distinct species in view of its morphological differences.

Citellus undulatus (Pallas). Ground squirrel.

Before any discussion of the Alaskan subspecies of ground squirrel, it is necessary to explain the application here of the name *Citellus undulatus* (Pallas) instead of *C. parryii* (Richardson).

Ognev (1947) reviewed the literature on the holarctic species of ground squirrel which occurs in Siberia and boreal North America. He quoted Heptner (1939) as being of the opinion that "the American susliks *Citellus parryii* (with subspecies), as well as *C. kodiacensis* All. and *C. osgoodi* Merr., are synonymous with *C. eversmanni* Brandt, and that by the rule of priority all susliks of this group should belong to the species designation *Citellus parryii* Richardson (1827) as the oldest." Ognev remarked that Argirupolo (*Priroda*, No. 1 (1939) p. 92) reached the same conclusion. Ognev (1947) pointed out, however, that the description by Pallas (1778) of "*Mus citellus* variet. *undulata*" has been overlooked. Consequently, this name antedating that of Richardson, it is necessary to apply the species name *C. undulatus* Pallas, 1778, "for all susliks of the *parryii-eversmanni* group in the character of the principal specific designation." Bobrinskiy *et al.* (1944) used the name *C. undulatus* for susliks which occur in the "Northern parts of North America and Asia. . . ." Ellerman and Morrison-Scott (1951) also accepted this application.

In revising the North American ground squirrels Howell (1938) made little effort to define the relationships existing between the *C. parryii* group and Siberian forms. He did state, in reference to *C. parryii ablusus* Osgood, that "This subspecies is closely similar to *C. buxtoni* (Allen, 1903b, p. 139) [=*C. undulatus leucostictus* Brandt, 1844] of eastern Siberia, differing chiefly in less intensely tawny coloration, and more blackish tail; in these characters *buxtoni* closely resembles *C. p. parryii*, which, however, is decidedly larger; since *buxtoni* intergrades in characters with *ablusus*, it may well be given subspecific status under the name *Citellus parryii buxtoni*." (p. 100). Allen (1903a) stated: "*Citellus buxtoni* finds its nearest relative in *Citellus barrowensis* (Merriam) from Point Barrow, Alaska. . . ."

In connection with the animal-borne disease investigations of the Arctic Health Research Center, a total of over 340 ground squirrels has been collected. I have observed all but one Alaskan subspecies in the field (exception: *C. undulatus nebulicola* Osgood). A small series of skulls of *Citellus undulatus leucostictus* Brandt, 1844, from Mys Emma (Emma Cape), northeastern Siberia, has also been available.

Through the study of this material, considerable new information has been obtained on the geographic distribution of the Alaskan subspecies of *C. undulatus*. The ranges of these forms have been plotted, using the locality records of Howell (1938) as a basis. Each form is shown on the distribution map (Fig. 9) and is considered separately below.

Citellus undulatus parryii (Richardson). (Fig. 9, No. 1).

Ground squirrels from the Romanzof Mountains and the vicinity of Arctic Village can be referred to *C. undulatus parryii*. This information changes somewhat the range concept as defined by Howell (1938) for northeastern

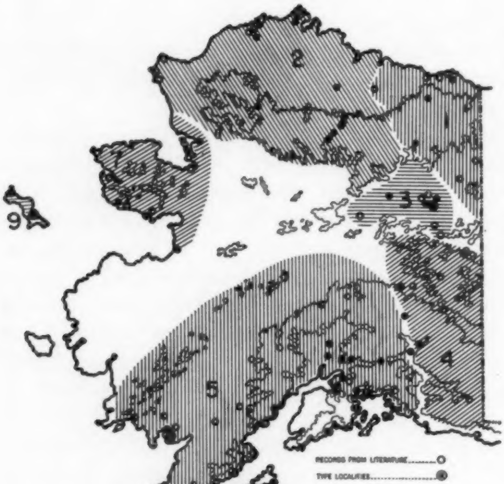

Fig. 9. Distribution of *Citellus undulatus* in Alaska: (1) *C. undulatus parryii;* (2) *C. undulatus barrowensis;* (3) *C. undulatus osgoodi;* (4) *C. undulatus plesius;* (5) *C. undulatus ablusus;* (6) *C. undulatus* ssp. indet.; (7) *C. undulatus* ssp. indet.; (8) *C. undulatus kodiacensis;* (9) *C. undulatus lyratus.*

Alaska. This form intergrades with *C. undulatus barrowensis* to the west, and with *C. undulatus osgoodi* to the south, near Arctic Village. The zone of intergradation with *C. undulatus barrowensis* cannot be accurately determined for lack of information from the region of the Brooks Range drained by the North Fork and Chandalar rivers. This squirrel was very abundant in the Romanzof Mountains during the summer of 1951. Five adult males, collected during July 1951 near Lake Schrader, ranged in weight from 514 to 893 grams (average: 656.6 grams). Four adult females ranged in weight from 638 to 885 grams (average: 718.5 grams).

Citellus undulatus barrowensis (Merriam). (Fig. 9, No. 2).

According to present knowledge, this form occurs throughout the Brooks Range and over the Arctic Slope except where it intergrades with *C. undulatus parryii* toward the east. The comparison of specimens from the central Brooks Range with topotypes (collected by E. A. McIlhenny, August 1897) in summer pelage showed good agreement. In winter pelage this squirrel shows much greyness (somewhat lighter than Mouse Gray) over the neck and shoulders. It is of interest that this squirrel has apparently disappeared from Point Barrow as a result of the permanent settlement of many Eskimo there in recent years. It still occurs, however, on the Inaru and Meade rivers, a short distance to the south. I have seen it near the coast about one hundred miles to the west of Barrow, and some sixty miles to the east.

A few observations on this form, not previously reported, have been made. A large adult male, very fat, weighing 723.5 grams, was killed by an Eskimo on 18 November 1951 near Tulugak Lake. The appearance of these squirrels above ground in the fall is intermittent after late September; I have no previous

record of any emergence later than October 1 (Rausch, 1951). For squirrels emerging in the spring, following hibernation, I have recorded a maximum weight of 977 grams. This animal, an old male, was collected on 6 May 1949, and measured 370 mm. in total length. Other males, some of greater total length, collected from 16 April to 6 May 1949, weighed from 530 to 816.3 grams (average for 7: 646.4 grams). Eight females, collected 20 May to 30 May 1950, ranged in weight from 439 to 616.5 grams (average: 548.2 grams). All specimens collected near Tulugak Lake.

Citellus undulatus osgoodi (Merriam). (Fig. 9, No. 3).

In reference to this squirrel, Howell (1938) stated: "It has a very restricted range along the Yukon River and although closely related to *parryii* apparently does not intergrade with it." Howell differentiated *C. osgoodi* on the basis of relatively minor characteristics (colour, size, and "audital bullae averaging slightly smaller and less inflated"). For some time I have considered this form conspecific with other Alaskan ground squirrels, despite its relatively isolated geographic range. As far as I have been able to determine, it inhabits river banks and other higher ground along the Yukon and Porcupine rivers, and is restricted essentially to the Yukon–Porcupine basin.

In June 1951 a rather large collection of mammals was made at Arctic Village. Among the ground squirrels obtained was a specimen which clearly shows intergradation between *C. osgoodi* and *C. undulatus parryii.* This specimen (orig. No. 10068), an adult male weighing 538.6 grams, was collected on June 19, and retains considerable winter pelage. It is intermediate in colour and tail length. Other specimens collected at the same locality showed more intense colouration than squirrels from the Lake Schrader region, but nevertheless were closer to *C. undulatus parryii.* This observation supports the conclusion that this squirrel should have only subspecific status.

With the longer tail, the total length of *C. undulatus osgoodi* is greater than that of any other Alaskan form of *C. undulatus.* However, the animal itself is not unusually large. The heaviest specimen I have examined, a male, collected August 1 on the Porcupine River, weighed 700 grams. Howell (1938) gave a maximum weight for males as 2¼ lbs.

Citellus undulatus plesius (Osgood). (Fig. 9, No. 4).

I have collected this squirrel in the Yukon Territory, and near the western limits of its range in Alaska. The latter may show some intergradation with *ablusus.* The Alaskan distribution as given here is essentially after Howell (1938), with additions from the recent literature (Baker, 1951; Strecker *et al.*, 1952). Slight modifications are made on the basis of topographic features, also. The zone of intergradation with *C. undulatus ablusus* Osgood may be rather extensive.

Citellus undulatus ablusus Osgood. (Fig. 9, No. 5).

The collection of a large series of ground squirrels in the Talkeetna Mountains and farther east has permitted some extension of the known range of this form. Although topotype specimens have not been compared, the

Talkeetna Mountain material compares well with examples from Unalaska and localities near the base of the Alaska Peninsula.

Howell (1938) referred squirrels from the Seward Peninsula to this form. According to his distribution records and my own observations, however, the Seward Peninsula population is separated from the main geographic range of *C. undulatus ablusus* by a wide region in the lower Yukon valley, within which apparently no ground squirrels occur (see Fig. 9, No. 7). Specimens have been obtained from Unalakleet, Nome, and Kotzebue in connection with the present work. It is true that these specimens agree in colour with *C. undulatus ablusus*. Tail length, however, agrees with *C. undulatus barrowensis*, with which intergradation probably takes place to the north. It appears that further study is needed before the Seward Peninsula form can be accurately designated. Quay (1951) referred his specimens to *ablusus*, probably on the basis of Howell's work.

Specimens from the lower Alaska Peninsula (Fig. 9, No. 6) cannot be assigned to *ablusus*, although Howell (1938) did so. The small series which I have at hand from the lower Peninsula is much paler in colour throughout. Osgood (1904) stated: "The Cold Bay specimens are not typical *ablusus*, but at present can be referred to no other form." This form appears to represent a distinct race; it will be described elsewhere.

Citellus undulatus kodiacensis (Allen). (Fig. 9, No. 8).

Howell (1938) considered the Kodiak Island squirrel to be specifically distinct from the mainland form. I do not agree that such a view is tenable, since structural differences are relatively slight. Early workers treated this form as a subspecies of *C. parryii*. Heptner (1939; cited by Ognev, 1947) concluded that *kodiacensis* and *osgoodi* were subspecies of *C. parryii*. It is treated here as a subspecies of *C. undulatus*.

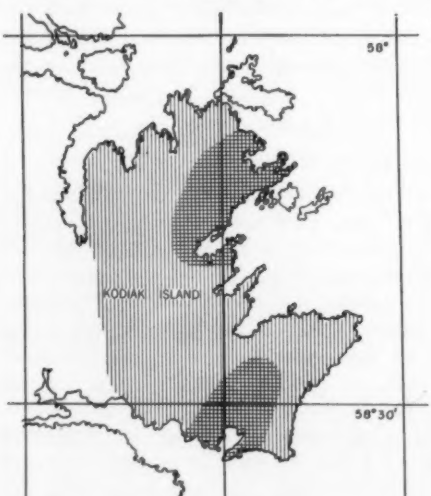

Fig. 10. Kodiak and neighbouring islands showing distribution of *C. undulatus kodiacensis*. Heavily shaded areas indicate known occurrence; lighter shading indicates probable occurrence.

It was stated by Osgood (1903) that this ground squirrel was thought to have been introduced on Kodiak from another island. Howell (1938), however, stated that the character of the Kodiak squirrel was such that it appeared to have been on the island for a long time. On the other hand, Hrdlicka (1944) did not find any ground squirrel bones during his excavations on Kodiak Island. It would seem that such would have been noted if squirrels had been present in earlier years. It is apparent that the range of *C. undulatus kodiacensis* is curiously restricted. I have not been able to make thorough observations on the island, but am certain that much suitable habitat is not occupied. Russell R. Hoffman, Refuge Manager, U.S. Fish and Wildlife Service, Kodiak, has kindly prepared a map of ground squirrel distribution (Fig. 10) insofar as he could determine from his own experience and from that of others familiar with the island. It is entirely possible that these squirrels were introduced on Kodiak. Further study is required to determine their origin, should this be true.[1]

Citellus undulatus lyratus Hall and Gilmore. (Fig. 9, No. 9).

The ground squirrel of St. Lawrence Island, of which more than 80 specimens have been collected in connection with this work, closely resembles *C. undulatus leucostictus* Brandt of northeastern Siberia. This fact was pointed out by Howell (1938). Study of both forms confirms this conclusion. This squirrel has been considered in more detail in another publication (Rausch, 1953).

There is need for additional *Citellus undulatus* material from Alaska if some points in geographic distribution of the various forms are to be clarified. This would be particularly desirable in regions rarely visited. It appears that the construction of highways may considerably influence the abundance and distribution of ground squirrels in Alaska. In this manner suitable continuous habitat is provided, along which the squirrels move.

Citellus undulatus has been widely studied in Siberia, and is receiving considerable attention in North America as an arctic species suitable for laboratory investigation. It is consequently of importance that workers concerned be acquainted with the circumpolar distribution of this species in order to take advantage of existing literature. Too often important knowledge is obscured by nomenclatural complexities and thus is lost to the highly specialized investigator.

A thorough discussion of the characteristics of palearctic forms of *C. undulatus* has been published by Ognev (1947). Cranial and external differences have been discussed in great detail, including also seasonal pelages of various subspecies. Ognev also reviewed the literature on the ecology and bionomics of the species.

[1]Field observations on Kodiak Island were continued for a period of one month, during May–June 1953. During this time, in late June, a single ground squirrel, apparently killed by a bear, was observed on a mountain at Karluk Lake by Alf Madsen, a professional guide. Mr. Madsen has had years of guiding experience on the island, and was much surprised to observe this squirrel so far from the known range of the species. The significance of this finding is not clear at present.

Tamiasciurus hudsonicus preblei Howell. Mackenzie red squirrel.

The tree squirrel of the Brooks Range, from Anaktuvuk Pass to the east, at least can clearly be referred to *T. hudsonicus preblei.* Comparisons have been made with topotype material (Fort Simpson, District of Mackenzie) and with material from other localities farther east. In addition to some 70 specimens from the central Brooks Range (see Rausch, 1951), about 50 additional animals have been collected from the vicinity of Arctic Village, Fort Yukon, and Beaver. An unusual occurrence of this species was recorded near Anaktuvuk Pass, far to the north of the taiga zone. Here, an adult female squirrel weighing 228.7 grams was killed on 7 August 1952, in the willows (*S. alaxensis*) by an Eskimo. This animal has been deposited, preserved entire, in the U.S. National Museum.

The occurrence of pale-coloured squirrels in the central Brooks Range was mentioned earlier (Rausch, 1951), and similar specimens were collected near Arctic Village. In general, they comprise a rather large proportion of the population. The most light-coloured specimen so far obtained was collected 6 December 1950, in the Savioyok valley east of Anaktuvuk Pass. It is briefly described:

Top of head and dorsum, except along midline, slightly darker than Ochraceous Buff. Along midline of last 2/3 of dorsum colour is near Xanthine Orange. Tail essentially Ochraceous Buff with lateral margins approaching typical dark colour; amount of dark colour greatly reduced, however. Ochraceous Buff of back becomes more buffy on the sides. Lateral stripe well defined, but grey rather than black. Face buffy; eye ring and nose buffy-white; cheeks greyish. Dorsal part of legs and feet approaching normal colour, but paler. Belly pure white.

Lemmus sibiricus trimucronatus Merriam. Brown lemming.

The brown lemming was abundant in the Romanzof Mountains during the summer of 1951. It was numerous on Barter Island during the same time, but was rare farther to the west. This seems to indicate that at least two distinct populations exist on the Arctic Slope. Farther west, in the Point Barrow region, the lemmings attained a high density in 1949 (see Rausch, 1950a), and then were scarce until the summer of 1952, when a moderately high density was again attained. Whether these animals will still be abundant during the summer of 1953 is difficult to judge. During December 1952, on a dog team trip of over two hundred miles along the Arctic Coast, I saw only one lemming on the surface of the snow. It was not possible to make adequate observations on conditions beneath the snow cover.

The Indians at Arctic Village could not provide any information on this species, and none was collected.

Ognev (1947) established that the Alaskan brown lemming is conspecific with the Obskiy lemming, known until recently as *Lemmus obensis* Brants, 1782. True (1885) had also referred the Alaskan form to *L. obensis. Lemmus obensis chrysogaster* was described by J. A. Allen (1903a) from the environs of Gizhiga, near the coast of the Sea of Okhotsk. Allen pointed out that it was similar to the Alaskan form; comparisons with Point Barrow specimens disclosed "no distinctive cranial differences." G. M. Allen (1914) described the

"little Kolyma lemming," designated as *L. paulus*, from near the mouth of the Kolyma river, and also reported *L. obensis chrysogaster* from Mys Bol'shoy Baranov, on the northeastern coast of Siberia. Ognev (1947) concluded that *L. paulus* is not distinct. Consequently, a single species of *Lemmus* occurs in Alaska and Siberia, with a second species, *Lemmus lemmus* Linnaeus, ranging from Norway, Sweden, and Finland, to the Kol'ski Poluostrov (Kola Peninsula), northwestern Russia.

Ellerman (1949) pointed out that the prior name of the Siberian lemming is *Mus lemmus sibiricus* Kerr, 1792. This animal, as cited from Kerr by Ellerman, was described as "of a smaller size, and a more uniform tawny color" than *Mus lemmus* (=*Lemmus lemmus*). The type locality of the former was given as the "Northern parts of the Uralian chain of mountains, and on the River Oby." Consequently, the name *L. sibiricus* is used here to designate the brown lemming of North America.

Lemmus nigripes (True) occurring on St. George Island, Pribilof group, has been considered specifically distinct from the brown lemming of Alaska. It was distinguished on the basis of slight colour differences, and by the fact that the auditory bullae are relatively small. Davis (1944) pointed out that this lemming is closely related to the mainland form, as well as to that of Nunivak Island. Davis concluded that "it seems best to treat *nigripes* as a full species." On the basis of comparisons, and in consequence of a broader view taken of the group, it does not seem justified to maintain *L. nigripes* as a full species. It is treated here as a subspecies of *L. sibiricus*.

North American forms of the brown lemming may be designated as follows:

Lemmus sibiricus trimucronatus (Richardson)
Lemmus sibiricus helvolus (Richardson)
Lemmus sibiricus alascensis Merriam
Lemmus sibiricus harroldi Swarth
Lemmus sibiricus nigripes (True)

A breeding colony of brown lemmings has been established in the laboratory at the Arctic Health Research Center. Kept under continual illumination for some months, a pair of lemmings began reproduction in late December 1952, and to date five litters, totalling 23 young, have been produced. These animals have become thoroughly adapted to confinement, and it is anticipated that there will be no further difficulty in maintaining them under laboratory conditions.

Dicrostonyx torquatus rubricatus (Richardson). Alaska varying lemming.

Varying lemmings were numerous in the Romanzof Mountains during the summer of 1951, and a small series was collected. No specimens were obtained at Arctic Village, but the species occurs there if one may judge from descriptions by the Indians. The people recognize a white "mouse" which in some years becomes abundant.

Ognev (1947) considered the North American collared lemming probably conspecific with the palearctic form. Ellerman and Morrison-Scott (1951) concluded that *D. torquatus* probably occurs in North America. In comparing skulls of *D. torquatus* with those of North American forms, Hinton (1926) stated that the former had "Upper incisors moderately heavy and much

more strongly curved than in *D. grœnlandicus . . .* those of *D. rubricatus* being apparently intermediate." In discussing *D. rubricatus,* Hinton stated further that "*D. rubricatus* is undoubtedly very closely related to the Old World *D. torquatus*, and until more material representing the latter is available, the status of *D. rubricatus* will remain doubtful."

The few specimens of *D. torquatus* which I have examined from northeast Siberia differ externally from Arctic Slope specimens only in greater intensity of colour. Colour is highly variable, both in Eurasia and in North America. Cranially there appears to be no differences of specific value, although there has not been adequate palearctic material available to establish average measurements. In view of the above-mentioned opinions, coupled with my own observations, I consider it appropriate to regard *D. groenlandicus* conspecific with *D. torquatus*. The names for North American races would consequently become:

Dicrostonyx torquatus rubricatus (Merriam)
D. torquatus groenlandicus (Traill)
D. torquatus kilangmiutak Anderson and Rand
D. torquatus richardsoni (Merriam)
D. torquatus exsul Allen

I have had no specimens of *D. hudsonius* (Pallas) available for comparative study, nor likewise any specimens of *D. unalascensis* Merriam. It is improbable that the latter has full specific standing. It was described on the basis of skulls from owl pellets, and apparently no comparisons with really adequate material have been made. G. M. Allen (1919) in his review of the American collared lemmings, after comparative study considered *unalascensis* a subspecies of *rubricatus*, since Merriam had previously compared it only with *D. hudsonius* at the time of its description. The external characteristics of this form were described by Gilmore (1933). *D. torquatus exsul* is considered in detail in another paper (Rausch, 1953). The Canadian varying lemmings were reviewed by Anderson and Rand (1945b), but these writers did not make any comparisons with palearctic material.

Clethrionomys rutilus dawsoni (Merriam). Red-backed vole.

Two specimens of this vole were collected at Lake Schrader, and a large series was trapped at Arctic Village. A single specimen trapped near the head of the Utukok River apparently constitutes the northwesternmost record of this species in Alaska. Farther west, specimens were collected at Nome and Kotzebue. A total of 240 specimens has been examined for helminth parasites (Rausch, 1952).

On the basis of present knowledge, a single form occurs over most of Alaska and adjacent Canada. Variation in pelage colour is considerable, so this character has little value in the differentiation of local races. I have also noted rather remarkable variation in size. However, Hanson (1952) has recently described a form from the Barren Grounds of the Perry River area, District of Mackenzie. Banfield (1951a) remarked that the tundra red-backed voles which he collected in northwestern Canada might be distinct. It is probable that the form to which he referred is the same as described by Hanson as *C. rutilus washburni*.

C. rutilus has a wide holarctic distribution. The status of the North American form was determined by Rausch (1950b). The Eurasian forms of *C. rutilus* have been studied by Ognev (1950). On the basis of more than 2,000 specimens, he was able to define the characteristics of palearctic subspecies. Ognev stated: "The colour of the fur is subject to great variations that depend on age, the season of generation of the animal, as well as on the geographical region from which the specimen in question came." He also reviewed the Russian literature in detail, summarizing considerable data on breeding, food habits, and habitat.

The red-backed vole is easily maintained in the laboratory. Breeding occurs regularly under favourable conditions.

Microtus oeconomus Pallas. Tundra vole.

A few specimens of *M. oeconomus* were collected near Lake Schrader, and a large series was obtained from the vicinity of Arctic Village. This vole occurs over all of Alaska, as well as in northwestern Canada as far east as Coronation Gulf.

Zimmerman (1942) demonstrated that *M. oeconomus* has holarctic distribution. Zimmerman's conclusions were confirmed by Rausch (1950b). In Siberia *M. oeconomus tshuktshorum* Miller occurs nearest Alaska, and *M. oeconomus operarius* Nelson is the North American form most closely related to it, according to Ognev (1950).

Rausch (1950b) listed ten North American subspecies of *M. oeconomus*. Setzer (1952) described *M. oeconomus gilmorei*, and Hall and Cockrum (1952) concluded that *M. amakensis* Murie is also only subspecifically distinct. Osgood (1909) described *M. endoecus* (=*M. oeconomus endoecus*) from the mouth of Charlie Creek, on the Yukon River. This subspecies was differentiated from *M. oeconomus operarius* and *M. oeconomus macfarlani* on the basis of certain cranial differences. Anderson (1937), on the opinion of R. C. Gilmore, concluded that *M. oeconomus endoecus* cannot be distinguished from *M. oeconomus macfarlani*, and consequently listed it as a synonym of the latter. Setzer (1952) stated that the two forms might be separable, on the basis of cranial differences. From the study of a large volume of material, it is concluded that Setzer's supposition is valid and consequently *M. oeconomus endoecus* is listed below as a distinct form.

A distribution map has been prepared for *M. oeconomus* in Alaska, excluding certain island forms whose range is well defined. The mainland races are discussed separately.

Microtus oeconomus endoecus Osgood. (Fig. 11, No. 1).

This form occurs over most of eastern and central Alaska, according to material at hand. Large series have been obtained from Arctic Village, Fort Yukon, and Beaver, as well as from other localities farther to the south and west. Comparisons of Lake Schrader and Arctic Village specimens with *M. oeconomus macfarlani* from Bathurst Inlet, Northwest Territories, indicate that the former are much closer to *endoecus* than to *macfarlani*, although there is some evidence of intergradation. I referred specimens from the

Fig. 11. Distribution of *Microtus oeconomus* in Alaska: (1) *M. oeconomus endoecus;* (2) *M. oeconomus operarius;* (3) *M. oeconomus yakutatensis;* (4) *M. oeconomus kadiacensis;* (5) *M. oeconomus* ssp. resembling *kadiacensis;* (6) *M. oeconomus macfarlani;* (7) *M. oeconomus innuitus.*

Anaktuvuk Pass region and Umiat to *macfarlani* (=*endoecus*) but Setzer (1952) (who also studied material collected here, deposited earlier in the U.S. Nat. Mus. collection) concluded that these specimens showed intergradation between *M. oeconomus macfarlani* (=*endoecus*) and *M. oeconomus gilmorei* Setzer. In Alaska, *M. oeconomus macfarlani* has a very restricted range (Fig. 11, No. 6).

From the material collected over northern Alaska, additional observations may be made on the status and distribution of certain forms. I first obtained a specimen of *M. oeconomus* from Point Lay, Alaska (topotype of *M. oeconomus gilmorei*) in the spring of 1949, and subsequently secured many more. A total of 187 specimens from this locality was examined for helminth parasites, and about 200 more were utilized in other ways. A good series of adult specimens has been assembled for study. Most of these animals were collected in late summer and therefore are comparable with most other Alaskan material in the collection here. Large series of voles were also obtained at Noatak, Deering, Unalakleet, and McGrath, and smaller series from Nome, Kotzebue, Wales, and Bethel. All of these specimens, in my opinion, should be referred to *M. oeconomus operarius* (Fig. 11, No. 2). The Point Lay specimens are relatively dark, and probably demonstrate intergradation between *M. oeconomus endoecus* and *M. oeconomus operarius.* I do not, on the basis of available material, consider *M. oeconomus gilmorei* distinguishable.

Microtus oeconomus ?kadiacensis Merriam. (Fig. 11, No. 4).

A series of voles collected near Skwentna, on the Skwentna River northwest of the head of Cook Inlet (Fig. 11, No. 5), closely resembles *M. oecono-*

mus kadiacensis. The Skwentna specimens are closest to Raw Umber above, with the sides near Saccardo's Umber, and Pale Drab-Gray underparts. Voles from Kodiak are more drab, with a tendency toward brownish. Osgood (1904) collected some voles which he referred to *M. oeconomus kadiacensis* along the coast of Bristol Bay and around the base of the Alaska Peninsula. Allen (1902) provisionally referred a vole from the tip of the Kenai Peninsula to this form. I have found those from near the base of this Peninsula to be referable to *M. oeconomus endoecus*, however. As far as I have been able to determine on the basis of limited material, all the Alaska Peninsula voles are of the same type – similar to *M. oeconomus kadiacensis*. It is possible that *M. oeconomus kadiacensis* is restricted to Kodiak and nearby islands. If so, voles from the Alaska Peninsula will have to be designated as a distinct subspecies. In any event, further study is needed.

Microtus oeconomus yakutatensis Merriam. (Fig. 11, No. 3).
This form has a restricted range in southern and southeastern Alaska. Some additional work is needed to define its range more accurately.

Previous attempts with three different forms of *M. oeconomus* to establish laboratory colonies, have been unsuccessful, but at the time of writing, however, a pair of voles, *M. oeconomus endoecus*, captured as subadults at Beaver, on the Yukon River, has produced a litter of 4. It is hoped that a breeding colony will be developed from this beginning.

Gilmore (1946) stated that *M. kamtschaticus* (=*M. oeconomus*) has not been observed to show distinct fluctuations in population density as contrasted with *M. miurus*. Quay (1951) commented briefly on this point. However, certain published records and my own observations do not support Gilmore's assumption. Allen (1902), writing of *M. oeconomus popofensis* Merriam, quoted J. D. Figgins that "Popof Island was literally overrun with these mice" during the fall of 1901. Bailey and Hendee (1926) mentioned that *M. oeconomus operarius* was reported as being "very common" at Cape Prince of Wales during the spring of 1922. Osgood (1904) found *M. oeconomus kadiacensis* "exceedingly abundant" at Nushagak. *M. oeconomus innuitus* Merriam (Fig. 11, No. 7) was abundant at the west end of St. Lawrence Island during 1950 and 1951. I found little evidence of this vole in the early spring of 1950, while there was still deep snow cover. However, E. L. Schiller, who continued observations the same year, found them "very abundant" after the snow was gone. We obtained more than 500 of these voles without difficulty for parasite studies. *M. oeconomus* was abundant at Point Lay in the spring and summer of 1951, and Utukamiut Eskimo have told me of having observed high densities. During the fall of 1952, *M. oeconomus endoecus* was at a high level of population density in the Yukon–Porcupine basin. The voles were especially abundant in the beds of old overflow lakes, and in many places the ground was nearly covered with soil loosened by their excavations. Consequently, it appears that *M. oeconomus* populations do fluctuate in density. Although Ognev (1950) gave detailed information on the ecology of *M. oeconomus*, nothing specific was included on population densities.

Microtus miurus Osgood. Narrow-skulled or gregarious vole.

The microtine subgenus *Stenocranius* Kastschenko is represented in North America by a single species, *M. miurus* Osgood. Five subspecies are recognized, of which three occur in Alaska. All inhabit arctic or alpine habitats. I have collected this species frequently, and considerable information on its Alaskan distribution has been obtained (Fig. 12). The Alaskan subspecies are discussed separately.

Microtus m. miurus Osgood. (Fig. 12, No. 1).

Reported previously only from the Kenai Peninsula (Osgood, 1901; Allen, 1902), I have collected this vole in the Talkeetna Mountains, about eighty miles north of Anchorage, as well as from the head of Palmer Creek, near the type locality. Colonies have been scattered and relatively small during the time of this work, as is characteristic when the population density is at a low level.

Since the habitat of *M. m. miurus* has not been described in detail, a few remarks are included here. The Kenai Peninsula colony was found near the head of a talus-covered valley, at an altitude of about 3,000 feet. At the highest point, the burrows had been excavated among the rocks, as well as in the open. The burrows were numerous, and runways extended down a steep slope for a distance of at least 200 metres. The plant association consisted essentially of *Luetkea pectinata* (Pursh) Kuntze, and *Cassiope Stelleriana* (Pall.), with *Phyllodoce ?aleutica* (Spreng.) appearing a few hundred feet below the highest level. A few other species of plants were interspersed—mainly *Carex* spp. and *Lycopodium* sp. The soil was moist, since flowing

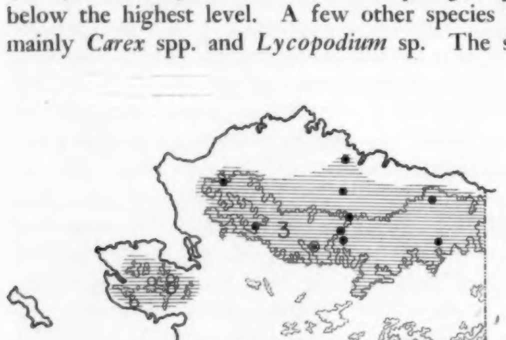

Fig. 12. Distribution of *Microtus miurus* in Alaska: (1) *M. miurus miurus*; (2) *M. miurus oreas*; (3) *M. miurus muriei*.

Fig. 13. Skulls of *M. miurus muriei*, wild-trapped specimens, showing cranial changes associated with growth. All males but the smallest. Second skull from left similar in stage of development to that of specimen described by Nelson as *M. muriei.*

springs were numerous in the immediate vicinity. The burrows were inconspicuous among the rocks, and it was only in the open that excavated soil was noted at the burrow entrances. These latter burrows apparently were storage chambers, since there was a heavy growth of *Carex* sp. nearby. The rhizomes of *Carex* are commonly stored by *M. miurus*. Dwarf willows were rare, and there was no evidence that *M. miurus* prepared "hay-piles" of willow or other plants for winter use.

The colony observed in the Talkeetna Mountains was found on the slope of a low mountain at an altitude of about 3,000 feet. Vegetation was dense, and the main species of plants were *Luetkea pectinata*, *Cassiope Stelleriana*, *Empetrum nigrum* L., *Salix reticulata* L., and *Salix* sp. Other plants, including *Vaccinium uliginosum* L., *Sanguisorba* sp., *Rubus* sp., and *Carex* spp. were interspersed. Larger species of *Salix* were absent. Here again there was no evidence of "hay-drying", although observations were made over a period of two summers.

It is probable that *M. m. miurus* occurs throughout the Talkeetna and Chugach Mountains. Much additional work is needed to determine its geographic distribution in southern Alaska.

Microtus miurus oreas Osgood. (Fig. 12, No. 2).

This form appears to be restricted in its distribution to the Alaska Range, where it was first observed in the Mount McKinley region. Here it occurs in the zone of mixed taiga–tundra as well as in the arctic–alpine zone. I have had but a few specimens of this vole, obtained through the courtesy of Dr. Adolph Murie. I have, however, had the opportunity of observing the habitat. This vole was described as an alpine species by Osgood (1907), who received

Fig. 14. Typical burrows of *M. miurus muriei* in *Salex alaxensis–Hylocomium splendens* association, Lake Schrader.

the prepared specimens from the collector. Detailed observations were given by Murie (1948), who first described its "hay-storing" habit. Recently this vole has been reported from Gakona Glacier, farther to the east (Strecker *et al.*, 1952).

Microtus miurus muriei Nelson. (Fig. 12, No. 3).

A single form of *M. miurus* occurs in the Brooks Range. Specimens from the Anaktuvuk Pass region served as the basis for the description of *M. miurus paneaki* (Rausch, 1950b). Nelson (1931) described *M. muriei* on the basis of a single immature specimen taken on the Kutuk River (see Fig. 13). Hall and Cockrum (1952) reviewed all the nearctic members of the *Stenocranius* group and concluded that *M. miurus paneaki* and *M. muriei* are conspecific. Since Nelson's name has priority, *M. miurus paneaki* consequently became *M. miurus muriei*, as pointed out by Hall and Cockrum. Figure 13 shows cranial growth changes in *M. miurus muriei.*

Three hundred specimens of *M. miurus muriei*, the majority from the central Brooks Range, have been examined for helminth parasites (Rausch, 1952). Series of specimens were collected in the Romanzof Mountains, and at Arctic Village. Three of these voles were trapped at the head of the Utukok River in the autumn of 1952, and unmistakable evidence of their occurrence was observed at the junction of the Cutler and Noatak rivers,

Fig. 15. "Hay pile" of *M. miurus muriei* near Lake Schrader, Romanzof Mountains. Composed exclusively of *Salix* spp.

although none was collected. Adam Leavitt, a Barrow Eskimo who lived for several years along the Arctic Coast east of Point Barrow, described characteristic "hay piles" which he observed along Fish Creek, just southeast of Teshekpuk Lake. These voles had previously been collected as far north as Umiat, on the Colville River (Rausch, 1950b).

The voles taken in the Romanzof Mountains were trapped mainly along the shores of Lake Schrader, where their burrows were located but a few feet above water-level. A large colony was found in a moist area along the north shore of the lake. The vegetation here consisted essentially of *Cassiope tetragona* (L.) and *Dryas octopetala* L., with several other species interspersed, namely, *Anemone parviflora* Michx., *Geum Rossii* (R. Br.) Ser., *Ranunculus sulphureus* Soland, and *Dodecatheon frigidum* C. and S. Along the lake margins *Petasites frigidus* L. was abundant, and *Therofon Richardsonii* (Hook.) was found in moist situations. Lichens and mosses were abundant.

M. miurus occurred abundantly in the willow–moss (*S. alaxensis–Hylocomium splendens* (Hedw.)) associations on the alluvial flats and along the stream at the west end of Lake Schrader. Twenty-four animals were taken from thirty traps over a single night. Willows (*S. alaxensis*) of rather large size occurred on the moss-covered hummocks in which the vole burrows were located (Fig. 14). The voles were present under similar conditions along Lake Peters. In no case was there evidence that they occurred at altitudes

appreciably higher than the lakes themselves, in contrast to what was observed farther to the west. It was here that the "hay-drying" habit was much in evidence. Large piles of willow twigs, some containing more than two thousand, were placed among and upon the trunks of *S. alaxensis* (Fig. 15). Four species of willow-twigs were represented: namely, *S. alaxensis*, *S. reticulata*, *S. barrattiana* Hook., var. *angustifolia* Anders., and *S. walpolei* (Cov. and Ball.) Ball.

At Lake Schrader, the roots of *Polygonum bistorta* L. ssp. *plumosum* (Small) Hult. [incorrectly listed as *P. viviparum* by Rausch, 1951] were stored by these voles.

Some Lake Schrader voles were trapped alive on 31 July 1951, and a colony has been maintained in the Arctic Health Research Center since that time. These animals persist in gathering all foods provided into a single "stock pile". As pointed out by Murie (1948) such activities are communal, all animals apparently taking part.

The Romanzof Mountain specimens, trapped in July and early August, were more grey in colour than is characteristic of summer specimens collected farther west. In general, specimens in winter pelage are relatively buffy in colour.

It has been possible to make limited observations on breeding and growth of the captive voles. Of the original 6 animals, all but 2 had died by 1 October 1951, leaving a single pair. On October 15 continuous illumination was provided (100 W bulb) with the hope that reproduction would be stimulated. A litter of 8 young was noticed on December 24, at which time they were estimated to be eight days old (on the basis of later observations). On December 28, at an average weight of 7.6 grams, solid food was being consumed. On 2 January 1952 the average weight was 12.6 grams; on January 14, 17.5 grams; on January 22, 41.2 grams. First signs of sexual activity were noted on January 18. At this time the parent animals weighed 57.8 grams (female) and 46.8 grams. The original pair produced a second litter of 6 on January 3, and a third litter of 7 on January 25. The young weigh from 2 to 2.8 grams at birth, and gain an average of 2 grams per day for the first twenty days. The young are very active, and run rapidly from the nest, when disturbed, even before the eyes open.

The largest wild-trapped specimen of *M. miurus muriei* that I have collected weighed 49.8 grams, with a total length of 161 mm. A captive male, however, attained a weight of 85.5 grams. An adult vole, laboratory-reared, is shown in Fig. 16.

Relationships:

Osgood (1901) concluded, largely on the basis of the enamel pattern of the molar teeth, that *M. miurus* is closely related to *M. abbreviatus* Miller, which occurs on Hall and St. Matthew islands. Nelson (1931) adopted this concept, and at the same time added *M. innuitus* (=*M. oeconomus innuitus* Merriam) to the *abbreviatus* group. Several subsequent workers have accepted this assumed relationship.

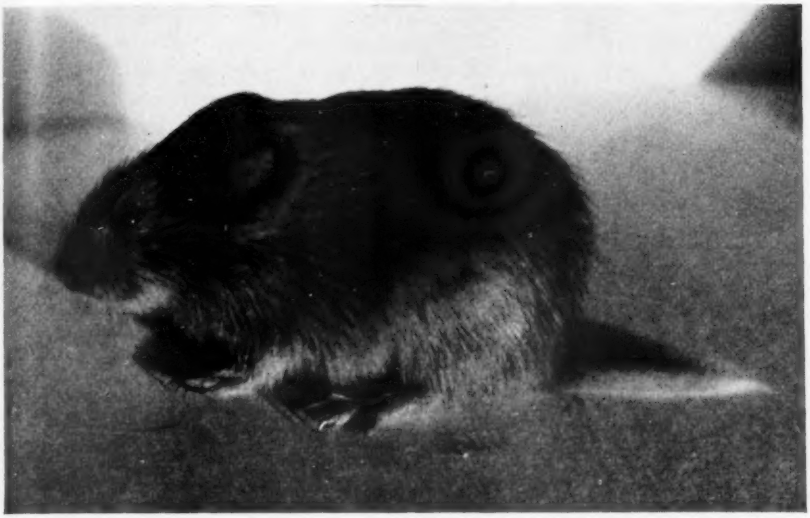

Fig. 16. *Microtus miurus muriei.* Subadult captive specimen. Note heavily-haired tail.

At the time he described *M. abbreviatus*, Miller (1899, p. 13) stated: "It is a rather large member of the typical group of the subgenus *Microtus*, and is more nearly related to a Siberian species which I suppose to be *M. kamtschaticus* (Polyakoff) than to any of the known Alaska members of the genus except *M. kadiacensis*." Bailey (1900) stated, in reference to *M. abbreviatus*, that "It belongs to the subgenus *Microtus*, and in general character comes nearest to the *operarius* group, from which it is excluded, however, by its unique molar pattern . . .". Zimmerman (1942) also compared *M. abbreviatus* with *M. oeconomus;* he concluded that it is closely related to *M. oeconomus*, but on the basis of molar pattern must be considered specifically distinct. Zimmerman pointed out that a grouping of *M. abbreviatus* with *M. miurus* is unnatural. The affinities of *M. oeconomus innuitus* are obvious, and I agree with Zimmerman regarding *M. abbreviatus*.

In order to determine the relationship of *M. miurus* to palearctic forms, comparisons were made with *M. gregalis* Pallas, the only Old World representative of *Stenocranius*. Specimens of *M. g. gregalis* Pallas, *M. gregalis raddei* Poliakov, and *M. gregalis brevicauda* Kastschenko have been obtained for this purpose.

It cannot be doubted that these animals are closely related. Externally, *M. gregalis brevicauda* is practically indistinguishable from *M. miurus*, even to hair texture and colour. They are likewise very similar cranially. However, there appears to be enough difference in palatal details to preclude the conclusion that they are conspecific (Fig. 17). A detailed description of *M. gregalis brevicauda* has been published by Dukelski (1928). Unfortunately, specimens of *M. gregalis buturlini* Ognev are not available. In view of its

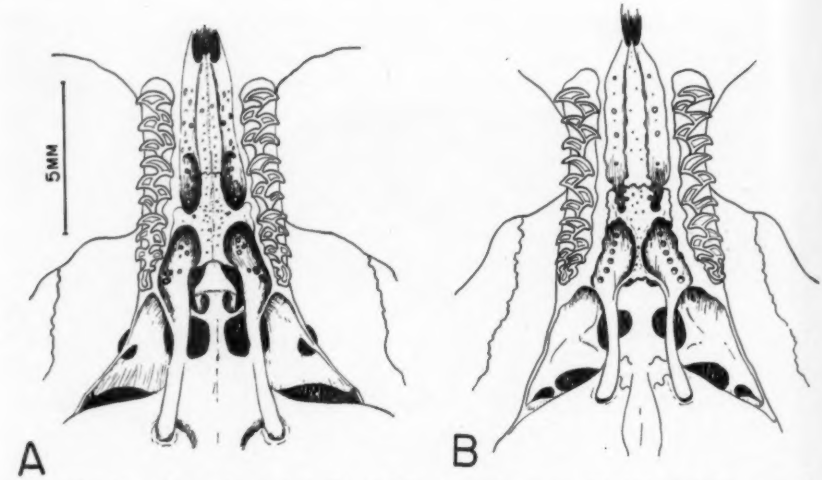

Fig. 17. Ventral portions of skulls of *Microtus miurus muriei* (A) and *M. gregalis brevicauda* (B), showing palatal details.

geographic distribution (northeast Siberia) it might resemble more closely the North American form. It may be concluded that the two species have been separated for a relatively long period of time, with the result that considerable divergence has taken place. Ognev (1950), in reference to the geographic distribution of the "gregarious field vole", stated: "The range is quite vast; from the Arkhangel'sk region to Chukotka and northern Alaska. . .". However, I cannot agree on the basis of material now available that they are conspecific.

The two species of *Stenocranius* described from northwestern Canada are *M. andersoni* Rand, 1945, and *M. cantator* Anderson, 1946. Hall and Cockrum (1952) concluded that these are also conspecific with *M. miurus*.

Castor canadensis canadensis Kuhl. Beaver.

Beaver occur in the vicinity of Arctic Village, where a few specimens were obtained. The northernmost limit of range of this species in the East Chandalar valley region has not been determined.

Two of the Nunamiut Eskimo, Kavik and Aknaniak, located a beaver dam near the head of Ikiakpuk Creek, a tributary of the John River. Although not as far north as the timbered Savioyok valley, where evidence of beaver was also observed (Rausch, 1951), this locality is neverthless well beyond the limits of taiga. This is unusual, not having been observed previously by the Eskimo nor otherwise reported insofar as I am aware.[1] Balsam poplar is common in some of the valleys on the south slope of the Brooks Range, and it would appear that this must be the only food supply of any importance.

[1]I have been informed by letter that Pat O'Connell, white trader now living near Anaktuvuk Pass, observed an adult beaver on about 25 June 1953 at the mouth of Inukpasukruk Creek, just south of Anaktuvuk Pass. This is certainly the northernmost record for this animal in the central Brooks Range region.

Ondatra zibethica spatulata (Osgood). Muskrat.

Muskrats are common around Arctic Village, where a small series was collected. I have no definite information on the northern limits of their range. Porsild (1945) found muskrats very common in the Mackenzie Delta, where they occur some distance north of timber-line.

Alces alces gigas Miller. Alaskan moose.

Not more than 3 or 4 moose are killed each year in the vicinity of Arctic Village. The species occurs more abundantly a few miles to the south, however. I have no information indicating how far north this animal may range in the eastern Brooks Range.

Bobrinskiy *et al.* (1944) included North America in the range of *Alces alces* and included *A. alces americanus* Clinton and *A. alces gigas* among forms discussed. Ellerman and Morrison-Scott (1951) included "Northern North America" in the range of the species. These authors recognized only two palearctic subspecies, however, against three recognized by Bobrinskiy *et al.* Recently, Peterson (1952) made a detailed study of the species; he concluded that two Old World and four North American races are valid.

Rangifer tarandus stonei Allen. Caribou.

Large herds of caribou were observed in the Romanzof Mountains in the summer of 1951. All had gone from the region by August 1, however, leaving deeply-worn trails as evidence of their passing.

Caribou regularly occur in the vicinity of Arctic Village during the late summer, according to the inhabitants. This herd travels east and west, leaving the Chandalar River region in September, and travelling east toward Old Crow, near the head of the Porcupine River. They begin to move west in early spring (usually April) and reach the Arctic Village vicinity in late July.

As far as I have been able to determine, three distinct herds occur on the Arctic Slope within the boundaries of Alaska. Farthest to the west is the Utukok herd, which apparently winters around the headwaters of the Utukok. According to the Utukamiut, who have hunted these animals for generations, the herds migrate south usually during December, and begin a northward movement about March. Since 1933–4 caribou have become increasingly abundant along the Arctic Coast in the vicinity of Wainwright, both summer and winter. Formerly, it was necessary to travel from forty to eighty miles inland to hunt caribou. Farther east, near Barrow, they were first noticed along the coast in about 1940, and since then have continued to increase. In December 1952, travelling for seven days on the trail from Barrow to Wainwright and back, I saw numerous caribou along the coast. No actual count was attempted, but one small group after another was observed, particularly in the region of Peard Bay. Observations made around the head of the Utukok and farther north in early October 1952, disclosed that caribou were numerous over the west end of the Arctic Slope. They appeared at this time to be travelling toward the southeast. Whether the regular occurrence of animals along the coast indicates an actual increase in the herd is difficult to say. The Eskimo are of the opinion that it does.

The Anaktuvuk Pass serves as a main migration route for the caribou of the Central Brooks Range. Migrations here have been discussed in some detail in another paper (Rausch, 1951). There is little reason to doubt that this herd maintains its integrity over the entire year, although the animals may scatter widely in small bands. Irregularity of migration is manifested in relation to the Anaktuvuk–John River valley, but this in itself is not significant because of numerous routes within the same general region.

The herd of northeastern Alaska apparently migrates partly northwest and southeast, and partly east and west, instead of essentially north and south as do the other two herds. The animals summering in the Romanzof Mountains region probably migrate southeast into the region around the head of the Porcupine River, southwest of the Richardson Mountains. The animals occurring in the summer in the lower Chandalar River valley, in the region of Arctic Village, migrate eastward toward the head of the Porcupine.

The essentially north–south movement farther to the west is related to the distribution of the taiga zone, within which most of the caribou winter. It is known that the central herd winters in the spruce forests on the south slope of the Brooks Range. It is evident, moreover, that this herd does not go south of the mountains, since observations in this region have been made over a long enough period of time to make this certain. Many caribou passed the winter north of the mountains, on summer range, during 1952–3. The cause of this behaviour is unknown at present.

Controversial opinions are often expressed on the status of caribou on the Arctic Slope. Since decisions regarding the utilization of these animals directly affect the aboriginal population, there is a need for serious and intensive study of the problem. Tangible evidence that the arctic caribou herds are diminishing has not been produced, nor has evidence to the contrary been forthcoming. The Eskimo express the latter belief, and one cannot ignore the judgment derived from a lifetime in the Arctic and their awareness of the importance of caribou for food and clothing. It is evident that existing information is relatively worthless insofar as this problem is concerned. It is apparent that certain important factors affecting caribou have undergone significant changes in recent years:

1) *Diminished importance of hunting by non-Eskimo*

The white population of arctic Alaska is relatively small. The whalers, who formerly utilized great numbers of caribou for food, are gone entirely. This was discussed by Banfield (1951b). For practical purposes, it may be said that no white men winter on the Arctic Coast under conditions requiring the utilization of game for food. Farther inland, with the decline in fur values, white men do little trapping. Prospectors are few in the Brooks Range and on the Arctic Slope, for various reasons. Almost every non-Eskimo along the Arctic Coast is now employed in one capacity or another by the federal or territorial government. These people do little if any hunting. Sport hunting in this region is insignificant.

2) *Decline in numbers of Eskimo*

The Eskimo are reduced in numbers, and those dependent almost entirely upon caribou exist as a pitiful few torn between their old ways and the white man's way of living. Only five settled places remain along the Arctic Coast north of Point Hope: Point Lay (50 Eskimo); Wainwright (200 Eskimo); Barrow (1,000 Eskimo)[1]; Barter Island (30 Eskimo); there is a single inland group in the Anaktuvuk Pass region (70 Eskimo). In addition, there is one family living at the mouth of the Colville River. The total number of Eskimo from the Brooks Range north is about 1,350 persons.

3) *Elimination of reindeer from the Arctic Slope*

According to information given me by people who had been actively engaged in the reindeer program at Wainwright and Barrow, there was at one time (about 1934) a total of about 22,000 reindeer in the Wainwright herd, and about 40,000 in the Barrow herd (1931). Today there is not a single reindeer remaining on the Arctic Slope except for some possibly running with the caribou. The animals were formerly scattered, in herds up to 4,000 to 6,000, from below Wainwright to Barter Island. According to all that I can learn, overgrazing along the Arctic Coast was evident by 1916, and reindeer camps in the vicinity of Barrow were often as much as seventy miles inland (across the Meade River). It is evident that elimination of reindeer has been in some ways beneficial to the caribou. It has also resulted to some extent in increased hunting pressure.

4) *Changed economy of the Eskimo*

At the present time, many of the Eskimo have an income which derives directly from permanent employment. Employment on the U.S. Navy Petroleum Reserve, at Point Barrow, is especially important, and has resulted in the large and ever-growing population of Barrow Village.[2] One now finds there people from villages as far away as Nome and Noatak, although the majority consists of people from the Barrow region, Wainwright, and Point Lay. Concentration in few villages and cash income affect caribou in two ways: 1) hunting is lessened in amount, since men with full-time employment have no time for it, and no need for doing so; 2) hunting pressure is local; the Barrow and Wainwright people both depend largely on the animals which come near the coast. Some Wainwright people travel up the Kuk to kill caribou, and the Point Lay people also hunt inland to a considerable extent. There is not, however, the generalized hunting pressure of former years. The inland people depend upon the caribou migrating through the Anaktuvuk–

[1]At the present time, as the result of the termination of oil exploration activities on the Arctic Coast by the U.S. Navy, there is no longer opportunity for employment of the coastal Eskimo. Consequently, all of these figures are subject to change.

[2]The population of Barrow Village is now decreasing since there is no longer opportunity for employment on the U.S. Navy Petroleum Reserve. Many of these people will return to the villages of their origin; others are going to Fairbanks and Anchorage to obtain work for which they have been trained. This situation may result in a greater dependency upon hunting, if other developmental activities do not provide opportunities for employment along the Arctic Coast.

John River valleys for their supply of meat and hides. The migration pattern during both 1951 and 1952 was such that few animals were available, with the result that for most of these years the people had to live on substitute food, mostly purchased from the white man.

Other controversial points have been discussed regarding the Eskimo-caribou relationships. It has been stated that the Eskimo of pre-firearm days were unable to kill many caribou. This view is not altogether tenable, for two reasons: 1) a great many more people lived inland and caribou were hunted much more both by them and by the coast people, since there were few substitute foods inland and nothing else suitable for clothing. 2) The Eskimo had developed some very effective means by which caribou were taken; two of these, the *kangigak* (corral) with snares, and the method of driving into a lake for spearing from kayaks were especially effective. The entire group took part in these activities. I have seen the latter method in use, and know that it is very effective.

The twelve families comprising the total Nunamiut (Inland) population still living in the old way maintain large dog teams. These are considered necessary; all are kept carefully tethered and all are used. Criticism of this practice can hardly be justified without providing an alternative way of life.

My experience in the region below the west end of the Brooks Range has been limited, so that detailed observations have not been made. The people of Noatak, Noorvik, Selawik, Shungnak, etc., occasionally have opportunity to kill caribou when there are irregular migrations, and this must be considered in evaluating hunting pressure on the Utukok herd, which presumably at times migrates well into the Noatak country. As far as I have been able to determine, however, caribou rarely come so far to the south. Some of the people travel inland to hunt. The kill by the Barter Island people and the Indians of Arctic Village, at the east end of the Brooks Range, is small. If the eastern herd is separate, as appears to be the case, this hunting has no effect of any importance.

Regardless of the factors discussed above, it must be recognized that for adequate clothing Eskimo must have caribou hides. It is well known that the hides of calves and cows, killed during the warm months, are most suitable. Winter boots of caribou legs are the only completely adequate type of footwear available, to Eskimo and white man alike, and the legs of 2 caribou are required to make one pair of boots. The skins of 2 cow caribou, or 3 calves, are required for a man's parka. For winter use, a double parka is needed, requiring from 4 to 6 animals. For a woman's parka, 2 large cow hides or 3 small ones are required, and for children a single skin is sufficient. Mittens and boot soles are made of hides of different types (winter skins for the former; thick hide of old bulls killed in the fall for the latter). There are other uses for caribou hides which are equally important, reported earlier (Rausch, 1951). Banfield (1951b) stated that 25 caribou hides are required annually by Canadian Eskimo to clothe a family of four.

Caribou may now be killed legally north of the Arctic Circle from August 20 to February 28. Calves are entirely excepted, and the legal kill

per hunter is 3 animals a year. It is obvious that it is impossible to obtain legally enough hides for clothing needs.

The attitude in Canada toward utilization of wildlife resources by the Eskimo is in contrast with that obtaining in Alaska. At the recent Conference on Eskimo Affairs[1]: "It was agreed that Eskimo should be encouraged and helped to live off the land and to follow their traditional way of life". These opposing views deserve careful analysis with respect to the eventual effect on both wildlife and aboriginal populations.

Caribou management cannot be discussed without some mention of wolf control, since in Alaska the one is the justification of the other. Indiscriminate destruction of carnivores has long been considered biologically unsound by leading ecologists, but the practice persists. Without discussing the place of the wolf as such in the biotic community, this opportunity is taken to point out the possibility that wolf control in Alaska may be contrary to the purposes of its advocates.

Palmer in 1926 pointed out that reindeer range, once depleted, may require as long as twenty to thirty years to recover. As a result of reindeer herding, there has already been some depletion of the range along the Arctic Coast. In the absence of an accurate census of the arctic caribou herds, and a lack of appropriate ecological studies to determine carrying capacity, range utilization, and migration patterns, it is not possible now to know whether an increase in the arctic herds would be desirable. Leopold and Darling (1952) have discussed the problem in detail. Wolf control without scientific basis is unwise at best, and may be detrimental.

The relationship of wolves and diseased caribou appears more important, and is tangible. In the northern countries where reindeer husbandry has been carried on for many years, hoof-rot has been an important disease. This disorder, occurring only in the summer, has many local names, and *Actinomyces necrophorus* Lehmann and Neumann (=*Spherophorus necrophorus* (Flügge)) is regarded as the causative agent. Hadwen and Palmer (1922) in regard to this disease in reindeer stated: "All foot troubles are serious when they occur in grazing animals; for as soon as the animal has difficulty in walking it can not feed properly and soon becomes thin and worthless. If the lameness is severe and likely to become worse it is the best policy to destroy the animal . . . the risk of passing on the disease is eliminated."

The causative organism, isolated from typical foot lesions in reindeer from a herd near Noatak, has been identified at the Arctic Health Research Center. It has not so far been isolated from caribou, but there is considerable evidence that it occurs in this animal also. Arthur H. Lachenbruch, U.S. Geological Survey, has kept accurate records during five summers of field work (1946–50) in the Brooks Range and on the Arctic Slope. During the last three weeks of August 1946 he observed a high prevalence of foot disorder in a caribou herd distributed along the lower Kurupa River and several miles down the Colville. He estimated the herd to number 20,000 animals, and concluded that at least 1 per cent of the animals was crippled. Dead animals were numerous, and

[1]"Conference on Eskimo Affairs." *Arctic*, Vol. 5 (1952) pp. 193-5.

still-living caribou could be run down on foot. The lesions he described to me were characteristic of *necrophorus* infection. Individuals in a herd observed in the late summer of 1947 on the Canning River showed apparently the same condition, as did animals observed near Lake Schrader in 1948. In the fall of 1952 there was a report of many crippled caribou having been seen by Navy personnel near the head of the Utukok River. Robert F. Scott, Biologist, U.S. Fish and Wildlife Service, and I attempted to locate these animals from the air, but were unsuccessful. In view of the vast country involved, and the number of caribou present, our failure to find the affected herd does not imply that the report was false.

On the basis of the above-mentioned records, it may be assumed that caribou are subject to a crippling hoof disease. Whether this is *necrophorus* infection is relatively unimportant. It is obvious, however, that rapid elimination of the diseased animals would be desirable to minimize infection. The Lapps and others have followed the practice of moving their herds to new, uncontaminated grounds following the outbreak of hoof disease. Wolves readily capture such afflicted animals. Moreover, wolf activities would probably result in continual movement of the normal animals, and the opportunities for infection would be minimized.

It is believed that the elimination of inferior animals from the caribou herds is an important function of wolves. Such factors should be taken into consideration when it is suggested that large-scale wolf destruction be practiced as a means to increase the numbers of caribou. It is significant that there is no indescriminate wolf control practiced in arctic Canada (A. W. F. Banfield, personal communication), where the knowledge of caribou ecology is far advanced over that in Alaska. The wolf is a part of the boreal fauna, and it has its place.

According to Bobrinskiy *et al.* (1944), the range of *Rangifer tarandus* comprises: "Zone of tundra and taiga of Europe and North America, islands of the Polar Sea." Ellerman and Morrison-Scott (1951) also recognized but a single holarctic species. There appears to be no justification for the use of the name *Rangifer arcticus* (Richardson) for the North American barren-ground caribou.

Ovis canadensis dalli Nelson. Mountain sheep.

Mountain sheep were numerous in northeastern Alaska during the summer of 1951. A few old skulls were found near Lake Schrader, but no specimens were collected. Sheep occur within twenty miles of Arctic Village. The animals of the eastern Brooks Range region are subjected to little hunting pressure.

Sushkin (1925) in a review of a paper by Nasonov, stated that *Ovis dalli* is conspecific with the palearctic *O. nivicola* Eschscholtz. Bobrinskiy *et al.* (1944) included North America in the range of *O. nivicola.* They recognized four palearctic subspecies, but did not discuss the North American forms. More recently, Ellerman and Morrison-Scott (1951) have concluded that both *O. nivicola* and *O. dalli* are conspecific with the North American *O. canadensis*

Shaw. Regarding this, they stated: "We also refer *nivicola* as a race to *canadensis*, though this is a purely nomenclatural difference; it is not clear why the Russians do not do likewise since they agree that the bighorn of North-Eastern Siberia and North-Western America are conspecific, and *canadensis* is the prior name."

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THE BOREAL LIMITS OF CONIFERS*

Ilmari Hustich†

THE expressions "forest-limit", "timber-line", or "tree-line" are all somewhat vague and difficult to define, and for the same reason it is not always easy to plot them accurately on a map. In the sense employed by North American writers, "timber-line" may mean the limit of commercially profitable forest utilization, the limit of forest in a biological sense, or simply the limit of trees. Sometimes it is not even easy to determine "when a tree is a tree".

Figure 1 shows the idealized trend of the different tree- and forest-limits. The local trend of these lines is similar whether near the polar, maritime, or altitudinal limit of trees. The principal difference being that as we approach the subarctic sea, or the vertical limit of trees, the lag between the vanguard of trees and the actual limit of continuous forest is slight, whereas in continental regions it is often very great. To understand the diagram, the following definitions may be helpful.

By "economic limit of forest"(I) is meant the limit beyond which commercial cutting of trees endangers natural afforestation. It is more or less what the past generation of Finnish foresters meant by the "*suojametsäraja*" or "*skyddsskogs*"-limit and also, at least in part, the "generative" forest-limit of Kihlman-Kairamo (1890) and the "effective" forest-limit of Sernander (1900) or Heikinheimo (1921).

By "biological limit of forest"(II) is meant the limit of continuous forest. In subsequent discussion this will be referred to simply as the "forest-limit". It corresponds to the "vegetative" and "empirical" forest-limits of Kihlman-Kairamo and Sernander.

By "tree-line"(III) is meant the absolute polar, maritime, or vertical limit of a given species in tree-form. The definition of what is meant by "tree" varies with different authors. According to some European writers a tree must be at least 5 metres high, whereas for subarctic regions Heikinheimo (1921) suggests 2 metres, providing that its trunk projects above the maximum snow cover of the locality.

The expression "polar tree-line" combines the most northerly limit of the

*This article is based on a paper which was published in Swedish in *Communicationes Instituti Forestalis Fenniae*, Vol. 40 (1952) pp. 1–20. Because this information was not readily available in English Dr. Hustich undertook to rewrite his paper for *Arctic*. Minor differences between the present maps and those published in 1952 are due to changes kindly suggested by E. Hultén (in a letter) [*Larix laricina* and *Abies lasiocarpa* in Alaska–Yukon; *Larix dahurica* on the lower Lena, and *Abies gracilis* in Kamchatka]. The writer also wishes to thank his friend, A. E. Porsild, Chief Botanist of the National Museum of Canada, who kindly edited the present paper, and suggested minor corrections to the maps.

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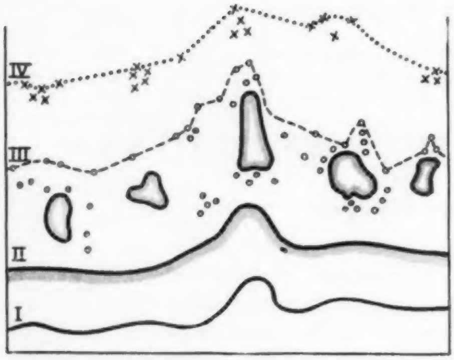

Fig. 1. Idealized trend of tree- and forest-limits: (I) Economic limit of forest; (II) Biological limit of forest; (III) Tree-line; (IV) Limit of species.

tree-like species of any forested area; it follows, therefore, that the polar tree-line in different areas may be formed by different species of trees.

By "limit of species"(IV) is meant the line of most advanced outposts attained by a species northward, seaward, or in a vertical direction, irrespective of whether growth is prostrate, ascending, or tree-like. Not infrequently the "tree-line" or "*Baumgrenze*" in the written accounts of explorers proves to be identical with the "limit of species", rather than with the "tree-line" in the sense given above.

Between the limit of species and the forest-limit is a transitional zone of varying breadth in which isolated trees as well as clumps of trees, or even small or large "islands" of trees, may occur. This transitional zone has been called "forest-tundra" and is the "*lyesotundra*" of the Russians. It may attain a breadth of over 100 kilometres but, especially in maritime regions such as for example the Atlantic coast of Labrador, may be replaced by scrub forest (Hustich, 1939). In my opinion the forest-tundra zone (ecotone, *sensu* Marr, 1948) phytogeographically constitutes the Subarctic proper, and the polar tree-line therefore represents the southern limit of the Arctic. In Rousseau's (1952) terminology, the forest-tundra is called "*zone hémiarctique*", whereas the northern spruce forests which were called "open boreal woodland" by Hare (1950) or taiga by Hustich (1949), according to Rousseau form the "*zone subarctique*".

The so-called "subalpine regions" or plains of northern Finland, Norway, and Sweden, which are dominated by alpine birch forest, should really be considered forest-tundra, being a direct continuation of the forest-tundra of the Kol'ski Poluostrov (Kola Peninsula). The word "subalpine" should, at any rate, be restricted to mean the vertical zone between the continuous evergreen forest and the alpine limit of trees, whereas the largely unforested Fennoscandian plateau is, in fact, a subarctic region in which scattered "islands" of forest and isolated trees occur.

Among the different "limits" discussed here, the "limit of species" is the one most easily mapped because most phytogeographers and foresters, who have visited the arctic and subarctic regions, have noted the outposts of tree species.

Figures 2–5 are mainly drawn from information contained in a number of published papers of which the more important are given in the list of references, and only in the Labrador-Ungava Peninsula, Hudson Bay region, and northern Fennoscandia has my own experience been incorporated (Hustich, 1939; 1948–50). It should be noted, however, that in some parts of the Arctic the northern limit of forest is not well known, and the lines shown are sometimes tentative. I wish to express my gratitude to Dr. Eric Hultén, who some years ago gave me sketch-maps showing the trend of the polar forest-limits in Eurasia. In the course of preparation of the present paper these sketch-maps have been brought up-to-date where needed. The polar limits for conifers in Fennoscandia are based on Hultén's atlas (1950).

Figure 2 shows the polar limit of the genus *Picea* (spruce) including *Picea Abies* (L.) Karst. (=*P. excelsa* Link), *P. obovata* Ledeb., *P. glauca* (Moench.) Voss., and *P. mariana* (Mill.) BSP.; the northernmost outposts in Alaska for *P. sitchensis* (Bong.) Carr are shown also. The genus *Picea* is, next to that of *Larix* (larch), the most important in the polar forest regions, although in Fennoscandia, this is not the case except in the Kol'ski Poluostrov.[1]

The specific status of the Siberian spruce, *Picea obovata,* has been questioned by Lindquist (1948) who thinks it should be called *P. Abies* var. *obovata* (Ledeb.) Fellman, whereas Russian taxonomists always consider it distinct. At any rate, the two species undoubtedly intergrade between the Kol'ski Poluostrov and the Pechora. I wish to call attention here to the striking similarity between *Picea obovata* and *P. glauca* in northern stations, where both species have short cones, rounded cone scales, and where the young twigs of *P. obovata* and *P. Abies* are sometimes glabrous.

Possibly future forest taxonomists will have to work with a circumpolar collective species of spruce, composed of *P. glauca* as ssp. "*americana*" and *P. Abies* as ssp. "*eurasiatica*" with the races var. "*europaea*" and var. "*obovata*"!

In North America, on the other hand, we have two clear-cut species, namely white spruce (*Picea glauca*) and black spruce (*P. mariana*). Although both have approximately the same northern limit, they are well separated taxonomically as well as ecologically. In forestry publications it is customary to designate the black spruce as the hardier of the two, but this is erroneous, at least in the Labrador-Ungava Peninsula. White spruce definitely ranges beyond black spruce near the maritime subarctic forest-limit in the Hudson Bay region, along the Atlantic seaboard, and in the interior of Ungava (Hustich, 1949; 1950). Where the two species occur together under extreme conditions, they may superficially be alike, although the annual shoot of the white spruce is always glabrous, while that of the black spruce is hairy. In exposed situations where black spruce occurs only as a prostrate shrub with abundant

[1]Although I have not been able to check Pachtusov's original record, it is of interest here to revive Middendorff's observation (1864, p. 543) that spruce was reported on Novaya Zemlya by the Russian navigator Pachtusov in 1842, who also recorded *Juniperus*, stating that the prostrate spruces he saw were even smaller than the dwarf birches growing on the island. "Wäre der Gewährsmann nicht von so erprobter Zuverlässigkeit, so hätten wir das Recht an dieser kaum glaublichen Mittheilung zu zweifeln, weil Nowaja-Semlja für baumlos gilt".

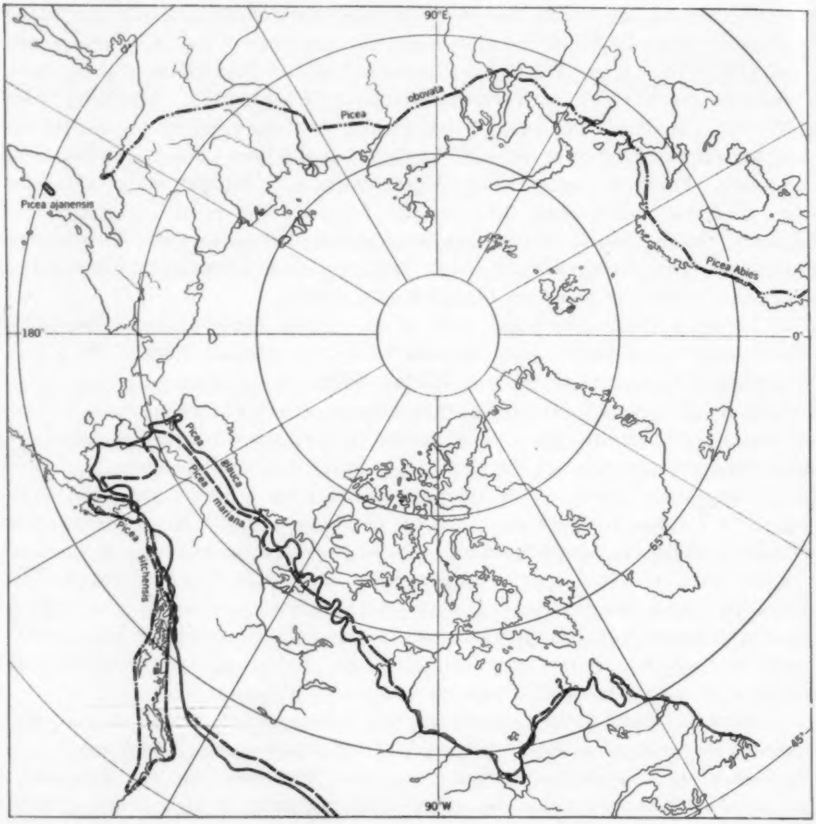

Fig. 2. The polar limits of the northern species of the genus *Picea*.

vegetative reproduction, the white spruce is tree-like. Farther south black spruce usually grows in acid bogs or muskegs, whereas white spruce grows on well-drained and generally richer soils. Both species may form extensive, uniform spruce–lichen forest, as may also the Siberian spruce near Noril'sk (Dedov, 1933; Hustich, 1951). While black spruce reproduces abundantly by layering, this is almost never the case with white spruce.

In *Picea glauca* two races occur in western Canada, namely *P. glauca* var. *albertiana* (Brown) Sarg. and *P. glauca* var. *Porsildii* Raup. In the area adjacent to Great Slave Lake and Mackenzie, Raup (1946) reported that *P. glauca* var. *albertiana* meets with a main species. Judging from the description, var. *albertiana* is not limited to western Canada and may prove to be a northern race of *P. glauca*. For this reason its northern limit has not been shown specifically in Fig. 2. *P. glauca* var. *Porsildii* (Raup, 1947) is the dominant spruce on alluvial soils in the Mackenzie Valley where it extends north to the Delta (Porsild, 1951).

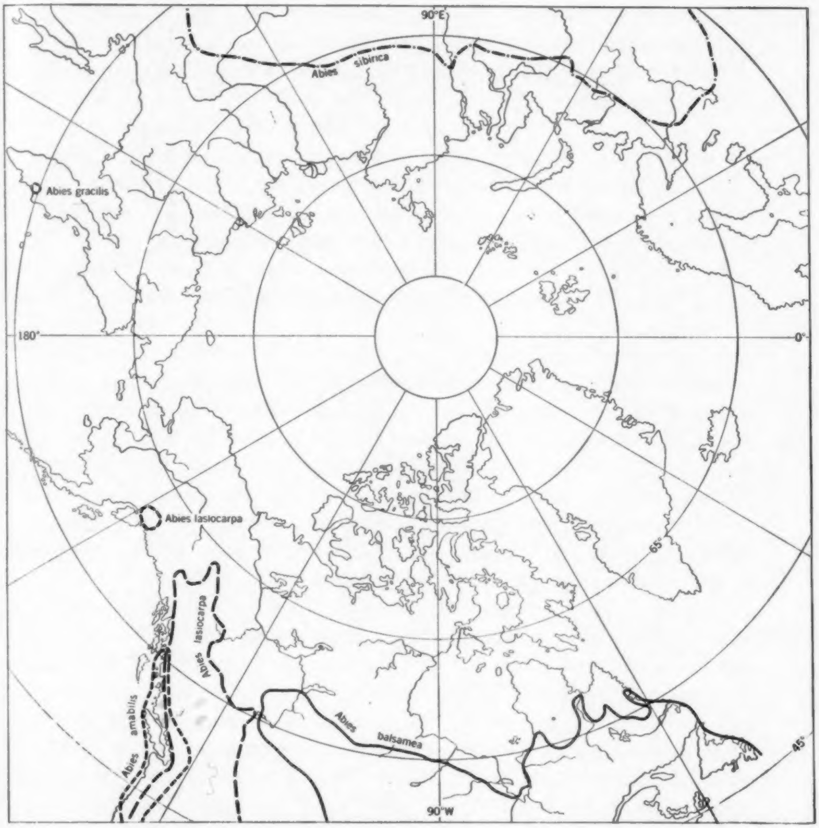

Fig. 3. The polar limits of the northern species of the genus *Abies*.

The genus *Abies* (fir) reaches the polar forest-limit only in Labrador along the Atlantic coast, extending almost to Ungava Bay (Fig. 3). Alaska, too, has a species of *Abies* but, otherwise, representatives of this genus reach only into the middle part of the taiga and are poorly represented in the northern parts of the evergreen forest.

The Siberian fir (*Abies sibirica* Ledeb.) is widely distributed in the Siberian taiga and in the valley of the Yenisey where it extends well beyond the Arctic Circle (Middendorff, 1864; 'Flora U.R.S.S.', 1934). It is a pronouncedly continental species with a range similar to that of *Pinus sibirica* (see Fig. 4). Ecologically, as well as in its ability to reproduce by layering, the Siberian fir simulates the balsam fir of Canada.

In Canada, *Abies balsamea* (L.) Miller ranges from the eastern slope of the Rocky Mountains to the Atlantic coast but is not as continental as *A. sibirica*, and is found on the islands along the Atlantic coast of Labrador where it enters the forest-tundra zone, without, however, reaching the polar tree-line.

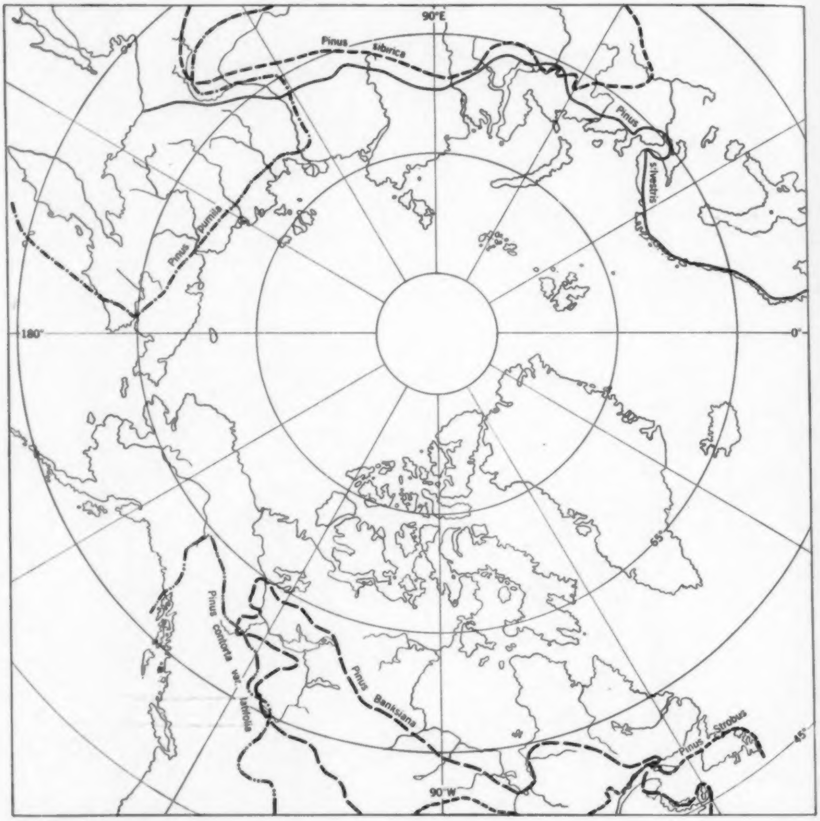

Fig. 4. The polar limits of the northern species of the genus *Pinus*.

The Cordilleran alpine fir, *A. lasiocarpa* (Hook.) Nutt., in the Yukon, ascends to 2,000 metres above sea level (Porsild, 1951) but does not extend into the polar forest-tundra.

Figure 4 shows the polar limit of the genus *Pinus* (pine) of which only *P. silvestris* L. and *P. pumila* (Pall.) Regel enter the forest-tundra region, while *P. sibirica* (Rupr.) Mayr, *P. Banksiana* Lam., and *P. contorta* Loudon var. *latifolia* Engelm. merely approach the polar forest-limit.

A remarkable feature of the Scandinavian polar tree-line is that the pine is the dominant conifer. Why spruce appears south of the pine west of the Kol'ski Poluostrov has caused much speculation among Scandinavian and Finnish forest-scientists. Some believe that the cause may be historical, i.e., due to ancient forest fires, others that it may be climatic. In North America the pine does not reach the subarctic seaboard either in Labrador or in Alaska.

Scotch pine (*Pinus silvestris*) occupies a large area, reaching from the Atlantic to the Sea of Okhotsk, although the pine which occurs in the eastern

part of this area is distinguished by Sukatschev as *P. silvestris* var. *jakutensis* Suk. The isolated populations of Scotch pine in the northernmost valleys of Norway are of great interest from a forest-genetical point of view, and deserve close study. They are the Scandinavian counterparts of the isolated "islands" of forest which occur elsewhere in the Subarctic.

P. sibirica, the Siberian cembra pine, is of continental range although recently two isolated stations (not shown in Fig. 4) have been discovered in the Kol'ski Poluostrov (Hultén, 1950; Nekrasova, 1951). At present it is not possible to determine whether these isolated occurrences are spontaneous. According to the reports of early travellers the seeds of cembra pine were formerly an important trade article and so much in demand that this pine was almost exterminated.

The Siberian dwarf pine (*P. pumila*) has a remarkable distribution. In stern Siberia it attains a higher latitude than that reached by pines elsewhere. Its ecology is very similar to that of *P. mugo* (*P. montana*) of the European Alps, although *P. pumila* belongs in the section *Pinaster* whereas *P. mugo* belongs in the section *Strobus*. *P. pumila* forms the polar limit of conifers in the Kolyma and Anadyr regions, but never reaches tree-size. Its distribution is included in Fig. 4. Its history and ecology have recently been investigated by Tikhomirov (1946) who points out that the species is "phytocenotically extremely strong", and a primary species wherever it occurs. According to Porsild (1939) *P. pumila* does not occur east of Bering Strait.

Jackpine (*P. Banksiana* Lam.) is the commonest pine of the boreal zone in Canada. It is a continental species reaching the sea coast only along the north shore of the Gulf of St. Lawrence and in Nova Scotia whereas the pine occurring in Newfoundland is the eastern white pine, *P. Strobus* L. The peculiar range of the jackpine in the Labrador-Ungava Peninsula is difficult to explain. One theory is that the species has not reached its climatic limit in the northeast. It should be noted that the cones of the jackpine open only after forest fires or during periods of exceptionally hot weather. Another interesting feature is that the jackpine, near its northern limit in Ontario near the Mattagami River (Smoky Falls), seems to grow taller than it does near its eastern and northeastern limit. In western Canada, jackpine reaches the Mackenzie Basin where it meets the lodgepole pine, *P. contorta* var. *latifolia*; but the range of neither extends into the forest-tundra.

Figure 5 illustrates the polar limit of the genus *Larix* (larch). For the Eurasian species I have followed Dylis (1948) who divides the Siberian larch into two species, *Larix sibirica* Ledeb. *s. str.* and *L. Sukatschewii* Dylis of which only the latter reaches the Kol'ski Poluostrov (Zinserling, 1935). Judging from the description, *L. sibirica* appears to be a non-aggressive species, restricted to shores of rivers and lakes, mountain slopes, bogs, and similar places (compare Sambuk, 1930), and the same may be true of *L. Sukatschewii*. It is interesting to note how closely Sambuk's description of the behaviour of the larch in the Pechora region parallels that of *L. laricina* in eastern Canada.

Larix dahurica Turcz., on the other hand, is an aggressive species which forms extensive forests in the eastern Siberian taiga, and entirely dominates

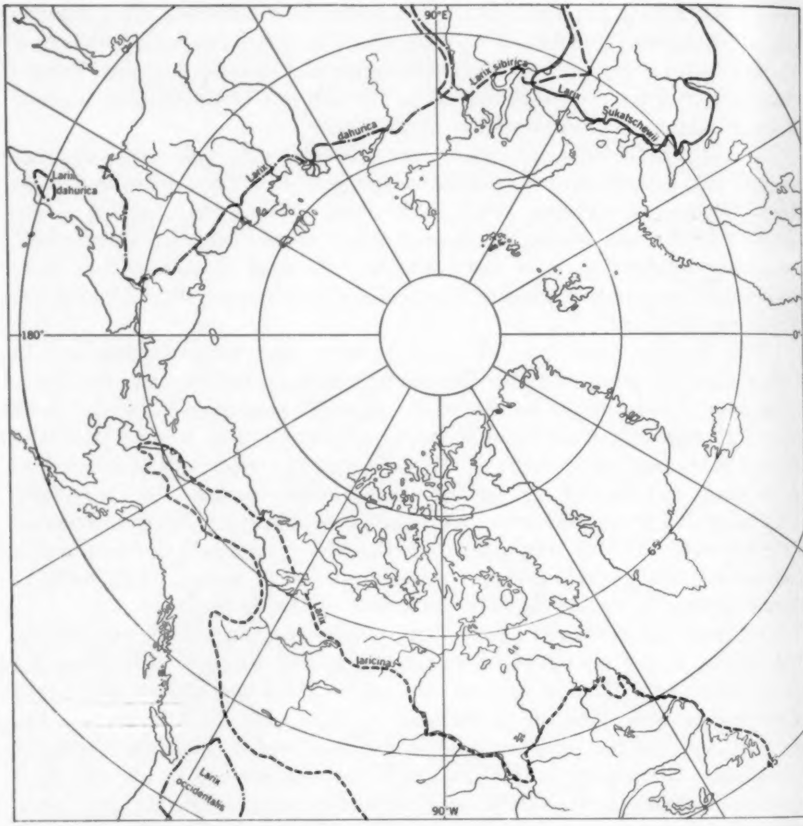

Fig. 5. The polar limits of the northern species of the genus *Larix*.

the region northeast of the Stanovoy Krebet (Stanovoy Mountains). *L. Cajanderi* Mayr, likewise credited to eastern Siberia, has been reported by Russian authors from the Yakutsk region and from northeastern Siberia. According to Ostenfeld and Larsen (1930) *L. Cajanderi* is synonymous with *L. Gmelini* (Rupr.) Gordon, which again is the same as *L. dahurica* Turcz. The range of *L. Cajanderi*, therefore, is not shown specifically in Fig. 5.

In Siberia, larches most often form the polar tree-line. In North America, *L. laricina* (DuRoi) Koch, although widespread in the forest-tundra, very rarely forms forests. In large bogs and fens in Labrador it may occasionally be the dominating species, and elsewhere may even form lichen forest; but across northern Canada *L. laricina*, together with white and black spruce, forms the polar tree-line. The Alaskan larch has been separated as *L. alaskensis* Wight, a name which has not been accepted generally, although Raup (1947) considers it a good geographic race, *L. laricina* var. *alaskensis* (Wight) Raup, and shows that it extends into northwestern Canada. Ostenfeld and Larsen

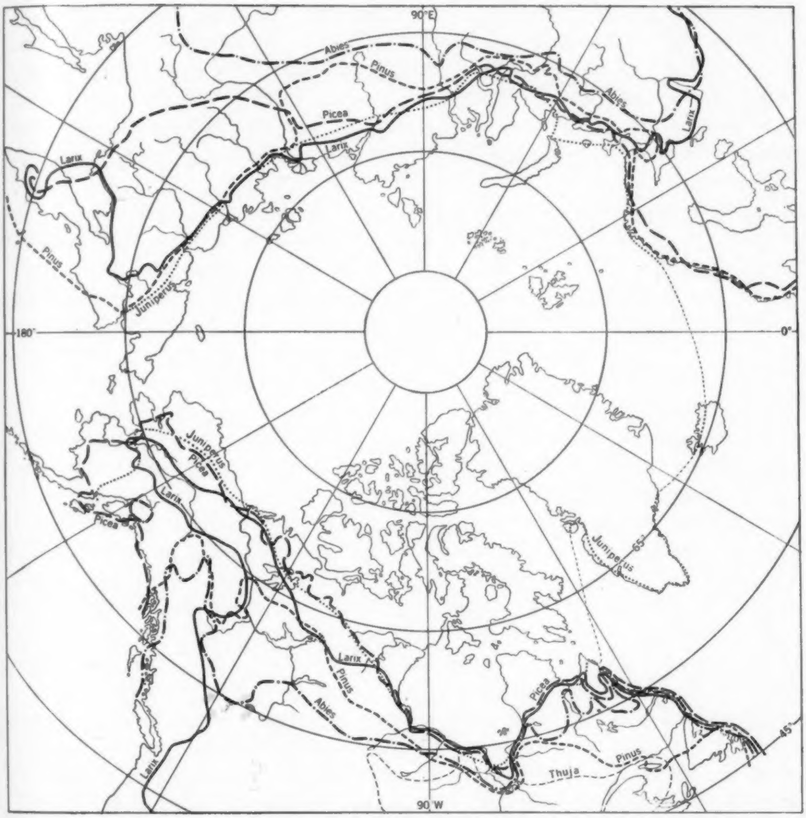

Fig. 6. The polar limits of *Picea, Abies, Pinus,* and *Larix* as shown on Figs. 2–5, and of *Juniperus communis* L. and *Thuja occidentalis.*

(1930), on the other hand, considered it only a trivial variation of *L. laricina.*

Larch generally avoids the sea coast. This is very noticeable in the Hudson Bay region where it is never found on the smaller islands. On the mainland, too, it is invariably found "behind" the black and white spruce. The same is true on the Labrador coast, in Alaska, in the Mackenzie Delta (Porsild, in letter), and in northern Europe.

In Fig. 6, showing the polar limits of spruce, fir, pine, and larch, I have added that of the juniper[1] (*Juniperus communis* L.), although it is never tree-like and occurs only as a dwarf shrub within the forest-tundra. It does, however, belong with the conifers, and for this reason I have shown its range in Fig. 6, but not in Fig. 7 which shows the polar tree-line. The common northern juniper is the only almost completely circumpolar conifer; it is the only conifer native to Greenland, Iceland, and Novaya Zemlya (see p. 151) and

[1] *Juniperus communis s. lat.* here includes var. *montana* Ait. as well as *J. sibirica* Burgsd. and *J. communis* var. *nana* Loud.

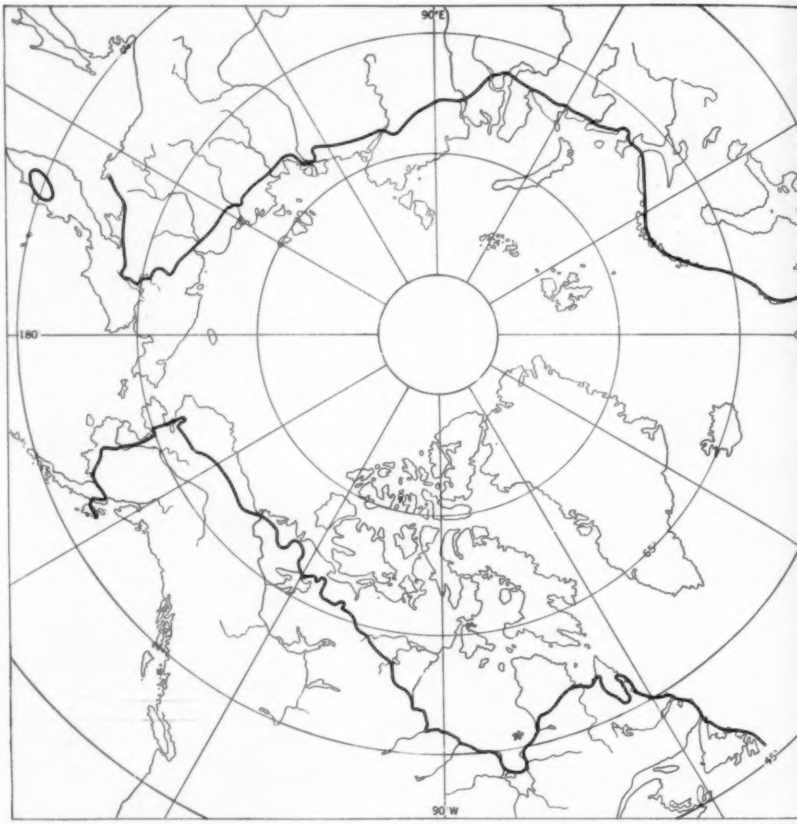

Fig. 7. The polar limit of tree-like conifers, irrespective of species.

the only one found in the Torngat region of Labrador and near North Cape in Norway.

Neither hemlock (*Tsuga*) or arbor vitaé (*Thuja*) reach the polar limit of conifers, even though the eastern white cedar, *Thuja occidentalis* L., does reach southern James Bay, and *Tsuga heterophylla* (Raf.) Sarg. and *T. Mertensiana* (Bong.) Carr., southern Alaska. But nowhere do they extend into the forest-tundra region. The range of *Thuja occidentalis* is given in Fig. 6.

Figure 7 combines the information given in Figs. 2–6, showing the polar limit of tree-like conifers, irrespective of species, omitting the not truly arborescent *Juniperus communis s. lat.* and *Pinus pumila*.

This paper deals only with conifers. If birch, alder, aspen, balsam, poplar, and tree-like willows were mapped, we would, however, obtain about the same picture, only the line would include Iceland and southernmost Greenland and extend farther north in Alaska and in easternmost Siberia.

For practical purposes, the line in Fig. 7 could, I believe, be called the southern limit of the Arctic, at least phytogeographically. Plant life is conditioned by climatic and edaphic factors, and the species itself is of little consequence because everywhere the northernmost individuals of coniferous tree species show almost the same characteristics. It is natural, therefore, that phytogeographers and climatologists (e.g., Miller, 1950) have tried to evolve a common equation or formula embodying the climatic requirements of all tree species at their polar limit. Hare (1952) has brought together the published information dealing with this problem, and in his map (p. 956) has synthesized the pertinent information. I have tried here to assemble the fundamental, although very approximate, phytogeographical data for the climatologists, and it may be helpful to add some remarks on the ecological character of the polar limits of conifers.

The polar limit of conifers is a phytogeographic boundary which is determined by the same general conditions that determines the boundaries of other species. As we approach it, we find a marked decrease in the edaphic amplitude of all species. That is, species are restricted to certain habitats. Thus, those that in the centre of their area are not pronounced calciphiles, near their northern limit are often restricted to habitats with calcareous soil. The distinct selectivity with regard to edaphic conditions of a given species near its northern limit is very noticeable in the forest-tundra where trees grow only on south-facing and well-drained slopes, in the valleys of rivers, in sheltered depressions, or on calcareous soil. In some parts of the forest-tundra this is not always so evident because fires and human activities may have disturbed the original distribution of trees. It is often possible, however, from the accounts of earlier travellers to reconstruct the original pattern of forest and forest islands in the forest-tundra.

Conditions favouring the formation of forest-tundra, and the occurrence of isolated islands of forest may vary in different parts in the forest-tundra; but the microclimatic factors are probably the most important. The human factor, however, in some places may have played an active part, as, for example, in the cutting of trees for fuel by arctic nomadic tribes. This is certainly the case in parts of northern Russia where the Samoyedy have caused great changes in the forest-tundra.

Isolated stands of trees in the northern part of the forest-tundra may possibly be relics from a warmer postglacial period, when continuous forest extended farther north than it does today. Thus, the present forest-tundra region of northern Scandinavia, Finland, and the Kol'ski Poluostrov may once have been occupied by continuous forest. Fossil evidence of former conifer forest is known to occur at elevations above and beyond the present polar limit of forest.

With regard to the probable migration of tree species in postglacial time Hultén (1937) stresses the importance of a former land connection across the Bering Sea. The different extent of glaciation in the southern parts of the Arctic and the northern parts of the Subarctic, as well as in the taiga region, must also be taken into consideration, as for example in Russia where the eastern

limit of larch more or less coincides with the eastern limit of the last glacial advance in northeastern Europe. During the last glaciation the most northern outpost of the Siberian taiga was in the region of Indigirka, well beyond the Arctic Circle (see Frenzel and Troll, 1952). This, and the fact that two ice sheets converged in the Stanovoy Krebet, certainly must have had a great deal to do with the present peculiar distribution of conifers in northeastern Siberia.

There have been several oscillations of the polar limit of forest in post-glacial time; some have lasted hundreds, some even thousands of years, while others have been of much shorter duration. Phytogeographical boundaries are notoriously unstable, and many species near their northern limits are most susceptible to climatic changes, even if of short duration, and particularly to changes in temperature. During the last decades there has been a fairly well marked amelioration of the climate of the forest-tundra region of northern Europe, and in northern Finland there has been a higher incidence of good pine seed-years during the nineteen 'twenties and 'thirties when the radial growth of trees likewise showed a marked increase (compare Mikola, 1952; and Hustich, 1948). A similar amelioration has taken place in the far north of Russia and Siberia (Ahlmann, 1948; Regel, 1950; *et al.*). But I am not so sure that this has been the case in subarctic Canada, where, at any rate, the amelioration has been less pronounced. Marr (1948) reported an advance of the tree-line in the Richmond Gulf area on the east coast of Hudson Bay, but my own measurements of the radial growth of the white and black spruce (Hustich, 1950) do not indicate a very distinct increase. Lysgaard's climatic map (1949) showing the latest world fluctuations likewise suggests that greater increases in temperature have taken place in northern Europe than in eastern Canada. Nissen (1951) has given a most interesting account of how this fluctuation has affected the reproduction of pine in northern Norway.

Although the coniferous forest, near its northern limit, is composed of different species having different ecological requirements, most of them react in a similar manner to the climatic conditions which characterize the southern boundary of the Arctic. The effect of wind and snow blast is similar and produces the same pattern of stunted growth in *Larix laricina* as in *Picea glauca* and *P. mariana*, or in *Pinus silvestris*. Reproduction, too, follows the same pattern in larch, spruce, and pine. In favourable years the incidence of florescence is by no means impaired, and may even be more intense than in places of more favourable climate. But there is a marked decrease in the production of viable seeds as we approach the polar limit of forest, and the conclusion reached by Renvall (1912), as well as by other Scandinavian and Finnish investigators, that viable seed is produced only in favourable years near the polar limit of forest, probably applies to all regions.

It is remarkable, on the other hand, that the ability to reproduce by vegetative means (adventitious root-formation, layering, and by vegetative shoots) is not universal among all species near the polar limit of trees. Thus, in Scotch pine and white spruce vegetative reproduction is rare, whereas in black spruce, balsam fir, alpine fir, and Siberian fir, it is the rule. The North American larch, likewise, readily reproduces vegetatively although dense scrub forest (*Krummholz*) is formed only by *Pinus pumila, Abies lasiocarpa, A.*

balsamea, and *Picea mariana*. Along the Labrador coast the scrub forest formed by black spruce and balsam fir may be as impassable as the "*Krummholz*" zone formed by the mountain dwarf pine of the central European Alps. Porsild (1951) has described similar *Abies lasiocarpa* scrub forest at timber-line in southeastern Yukon.

The composition of the forest-tundra of northern Europe differs in many respects from that of other parts of the Subarctic. In northern Scandinavia birch (*Betula tortuosa s. lat.*) is forest-forming whereas the birches of North America and Russia are not. In North America, on the other hand, especially in the Mackenzie District, in the Yukon, and in Alaska, alder (*Alnus crispa*) may form dense scrub forest even beyond the northern limit of spruce (Porsild, 1939). The same is the case on mountains along the Labrador coast. Various deciduous species occur in the forest-tundra but they are not forest-forming, except in the Anadyr region where *Populus suaveolens*, *P. tremula*, and some arborescent willow and birch species form a deciduous forest beyond the *Larix dahurica* forest. A comparison of the birches of the Old and New worlds is difficult because the nomenclature of the genus *Betula* in different parts of the Arctic and Subarctic is in urgent need of clarification.

The farther north one travels, whether in America or Eurasia, the greater becomes the percentage of circumpolar species in the flora; likewise, the similarity of the dominant vegetation types becomes more pronounced. It is surprising, therefore, that not a single arborescent species is circumpolar, even though several birches of the forest-tundra may be closely related. Not even the dwarf birch, *Betula nana*, is circumpolar, for in some parts of the Subarctic it is replaced by species of similar growth habit and ecology (*B. exilis* and *B. glandulosa*). Only *Juniperus communis* (incl. vār. *montana*) is almost completely circumpolar, except for a gap in the Bering Sea region.

Considering the great similarity between the boreal forests of the Old and New worlds it is equally remarkable that none of the Eurasian conifers occur in eastern North America and that white spruce has not reached eastern Asia. Perhaps taxonomists and phytogeographers dealing with the taxonomy of boreal tree species have been unduly impressed by the importance of the Atlantic Ocean and Bering Strait as phytogeographic barriers. At any rate, it is fairly well agreed that, with the exception of the quite distinct black spruce, the Eurasian and American spruce and larch species, which form the polar limit of conifers, must be rather closely related.

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[1]A more complete list of papers dealing with the polar tree- and forest-limits will be found in Hustich (1952).

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INSTITUTE NEWS

Death of W. R. B. Battle in Baffin Island

On July 15 P. D. Baird, leader of the Institute's Baffin Island expedition, sent out a message that W. R. B. Battle had been drowned in a glacial stream on July 13. At the time, Battle, who was the glaciologist on the expedition, was returning alone from a walk in the Pangnirtung Pass area near Base Camp B. His body was found after a search lasting one-and-one-half days, and has since been buried on the moraine above Summit Lake.

W. R. B. Battle came out from England in 1952 to take up the Senior Fellowship under the McGill University–Arctic Institute Carnegie Program. His fellowship had been renewed for the year 1953–4.

A short note follows on the work of the Baffin expedition.

Baffin expedition 1953

This year the Institute has sent a party led by P. D. Baird, Director of the Montreal Office, to the Cumberland Peninsula of Baffin Island. As in the 1950 Baffin expedition, the Swiss Foundation for Alpine Research is cooperating and has sent four men to take part in the expedition.

The region being studied this year is some 300 miles southeast of the Barnes Icecap, explored three years ago. Glaciological and geomorphological work is being carried out on the Penny Highland ice cap and in the Pangnirtung Pass area. Botanical and zoological studies will mainly be made in the Pass area. At the same time Professor V. C. Wynne-Edwards, who has also received a grant from the Institute, is carrying out ornithological studies around the coast of the Cumberland Peninsula.

The party of thirteen scientists left Dorval airport, Montreal, at 9.30 a.m. on May 12, flying in an R.C.A.F. North Star aircraft to Frobisher. They reached Frobisher at 20.00 hours, where the chartered Norseman aircraft was awaiting them. By May 13 all members of the expedition and their equipment had been flown from Frobisher. The following two days were spent sorting and repacking stores, shipped up last summer, for inland flights. On May 16 Base Camp B, 1,300 feet, was established by aircraft at the northeast corner of Summit Lake, 66°40N., 65°08W. Later in the day Camp A1, 6,700 feet, was established on the Penny Highland ice cap at 66°59N., 65°35W.

Foggy weather hindered flying operations until May 20 when Camp A2, 6,000 feet, was established at 66°50N., 65°15W. The same day Watson (zoologist) and Kidd (geologist) were flown to Padloping for two weeks sledging in that area. On May 23, when weather permitted, additional flights were made to camps B and A2, and J. Thomson travelled by dog team to cache a canoe at the head of Pangnirtung Pass. Hugh Thompson (geomorphologist) left by dog team on May 25 for the head of Pangnirtung Fiord to make soundings before walking back to base. The Norseman aircraft returned to Churchill on May 26.

On June 14 a message was received that the Biological Camp had been set up in Pangnirtung Pass at 66°45N., 64°41W., and that Watson and Kidd had arrived at this camp after a successful visit in the Padloping area and "a hard slog over to Pangnirtung Pass". The Swiss glaciologists had finished their seismic work at Camp A2, where 100 feet of firn was found on 600 feet of ice, and had moved to Camp A3 at 66°48N., 65°04W. on foot carrying their equipment. There was a blizzard in the vicinity of A1 on June 14 which compelled

P. D. Baird to spend a night in an igloo about 600 yards away from the camp. The maximum temperature experienced up to June 14 at Camp A1 was 26°F and the minimum -13°F.

Gifts to the Institute

The Librarian would like gratefully to acknowledge donations to the Institute Library from the following friends and Associates: Mr. Louis Bailey, Mr. Gerald Birks, and Mrs. R. A. Davies.

Mr. Ross Hennigar has kindly donated a caribou-skin parka to the Museum.

The Institute would also like to express its appreciation of a display on loan to the Museum from the Iron Ore Company of Canada.

NORTHERN NEWS

Award of Royal Geographical Society's gold medals for 1952

The Royal Geographical Society has announced that Her Majesty the Queen has approved the award of The Founder's Medal to P. D. Baird, Director of the Montreal Office of the Arctic Institute of North America, for explorations in the Canadian Arctic, and The Patron's Medal to Count Eigil Knuth, leader of the Danish expedition to Peary Land 1948–50, for explorations in northern Greenland and for his contributions to Eskimo archaeology.

Banks Island party

Early in May, T. H. Manning, accompanied by Capt. I. M. Sparrow of the Royal Engineers, England, left Edmonton by R.C.A.F. aircraft for Sachs Harbour, Banks Island, to continue a coastal survey of the island for the Defence Research Board of Canada. Last summer Mr. Manning, accompanied by Andrew Macpherson, had begun the survey by canoe along the west and north coasts. At Castel Bay they were forced by an early freeze-up to leave their canoe and return overland to Sachs Harbour. This year Mr. Manning hopes to complete the trip around the island. On arrival in Banks Island the party planned to transport their supplies by Eskimo dog team to Castel Bay.

Ellesmere Ice Shelf party

In April 1953 a two-man party began a study of the ice shelf of northern Ellesmere Island. Geoffrey Hattersley-Smith, Defence Research Board of Canada, and Robert Blackadar, Geological Survey of Canada, were flown to Thule by U.S.A.F. aircraft, in order to pick up two Eskimo and their dog teams. They then continued by air to Alert where they planned to start their survey, returning in the fall.

Hattersley-Smith will make a glaciological study of the ice shelf, which is believed to be the source area of the arctic ice islands.[1] He plans to measure the extent and thickness of the shelf and to determine whether it is at present increasing in size. Blackadar will assist this work and will also examine the geology of the coastal belt.

Ice islands observed on R.C.A.F. polar flights

During this year's polar flights by the R.C.A.F. Specialist Navigation Course from the Central Navigation School, the following information on ice islands was obtained.

On 25 April a reconnaissance of T1 was carried out while on a flight around

[1]See *Arctic*, Vol. 4 (1952) pp. 67–103, 183–7, and 211–23.

Ellesmere Island. T1 was found at the entrance to Yelverton Bay on a bearing of 308° True and 27 miles from Mitchell Point, about 100 miles farther west along the Ellesmere Island coast than its position on 28 April 1952. Its shape and size had not changed. There is a possibility that T1 may ground on the west side of Yelverton Bay east of Alert Point as it is only about 5 miles from the shore and its westward movement appears to be blocked by Alert Point.

Also on the same flight a small ice island (approximately 2 by 4 miles) was sighted about 8 miles northeast of Franklin Island in Kennedy Channel. This island, the first to be sighted in the channels between Ellesmere Island and Greenland, had the distinctive corrugated pattern and was easily spotted among the old ice floes. At the time Kennedy Channel was covered by a sheet of rough ice.

On 26 April, while returning from a flight over the Pole, an ice island was sighted through the clouds just off the west coast of Axel Heiberg, between Good Friday Bay and Skrugar Point. Although reconnaissance was very limited the island appeared to be about 4 by 8 miles and was easily recognized by its undulating surface. This island is the largest discovered to date along the west coast of Axel Heiberg.

KEITH R. GREENAWAY

Blue Dolphin Labrador expedition—winter project 1953

During March and April 1953 an expedition led by David C. Nutt and sponsored by the U.S. Office of Naval Research and the Arctic Institute carried out oceanographic studies of the winter regime in the tidal estuary of Lake Melville, Labrador. This was a continuation of investigations on the Labrador coast for the past four summers[1] and of the 1952 winter expedition to Lake Melville.

The expedition flew from Westover, Mass., to Goose Bay with the U.S.A.F. on March 11, and on the 13th made a reconnaissance flight to observe ice conditions in Lake Melville and Hamilton Inlet. All personnel and equipment were then transferred by snowmobile to the settlement of North West River, which was the base of operations.

The party worked in two groups: David Nutt, Weston Blake, and two local guides spent sixteen days on a 300-mile trip by dog team along the south shore of Lake Melville to The Backway, Rigolet, and Hamilton Inlet, returning by Double Mer and the north shore of Lake Melville. Five oceanographic stations were occupied in Lake Melville and two in The Backway. In all areas the ice was found to be thinner than in the previous year. The maximum thickness measured on the lake was 35 inches, the minimum 9 inches, with the average around 25 inches. The maximum depth of snow on the lake was 24 inches, but wind had blown much away. An exceptionally early thaw this year enabled the party to occupy one station in Hamilton Inlet by boat.

The second party, consisting of Lawrence Coachman, John Snyder, and one guide worked at the western end of Lake Melville. Volume and flow measurements were made on the Kenamu, Hamilton, Goose, and North West rivers; in the last locality working from a boat, as this river remains open most of the winter. Four stations were occupied in Goose Bay, Terrington Basin, the Hamilton River, and Grand Lake. All oceanographic stations had previously been occupied during summer or winter visits to the area, except the one on Grand Lake. Snyder carried out studies of ice around North West River and Goose Bay, and photographed thin sections of ice to show crystal structure. Blake also continued his 1952 studies of the forest types and physiography in this area.

The various temperature profiles obtained indicate that warm layers are present in Lake Melville during the winter, particularly at the western end of the lake, while the water of Hamilton Inlet is uniformly cold.

The weather until late March was

[1]An account of this work during 1949 and 1950 written by David C. Nutt was published in *Arctic*, Vol. 4 (1951) pp. 3–11.

excellent, with little wind and only a few partially cloudy days. Temperatures were usually below freezing and a minimum of -12°F was recorded. Occasionally temperatures rose above freezing in the afternoon. However, in late March and April the weather became considerably warmer, and water and slush on top of the ice made travel difficult. The inner part of Hamilton Inlet was completely free of ice by April and the ice in the lake was breaking up rapidly. All indications pointed to an unusually early shipping season.

Both parties travelled by dog team—the first used a specially designed pyramidal tent which fitted over the oceanographic frame, and the other a Labrador-style wall tent. Portable wood-burning stoves of local manufacture were used for cooking and heating the tents and proved very satisfactory. One member of the party tried skis, which are seldom used in Labrador, and found them excellent for fast travel on the lakes. However, the wide Indian snowshoes are indispensable for camping and travel in the deep snow of the forests, as well as for beating down a trail for the dogs in deep snow.

In early April further sledging proved impossible, and the party was ferried back to Goose Bay by helicopter. It was originally hoped to continue the work in the Nain area of the coast, but this plan had to be abandoned because of the early thaw, and the party returned to Westover on April 10.

Sheep farming in Greenland

The following note was written by Miss M. C. Findlay, who spent the summer of 1952 *in west Greenland studying sheep farming on a research grant from the Institute.*

There are now 30 full-time and 250 part-time sheep farmers in the southernmost district of west Greenland. Many Greenlandic families are profiting by the addition of mutton to their diet, home-knitted sweaters have replaced sealskin anoraks among the most prosperous, and in the innermost parts of the fjords real farms, with sheep stalls, homefields, and vegetable gardens, are to be seen.

By the turn of the century the seal hunting that had been the mainstay of Greenlandic life was so impoverished that the west Greenlanders were facing grave difficulties. A substitute occupation was becoming an urgent necessity, and in 1915 the Greenland Department sent one Dane and a flock of 175 Icelandic sheep to west Greenland as an experiment.

Work was undertaken along two lines: hunters were encouraged to loan from 10–20 sheep from the new Sheep Breeding Station and to start keeping sheep as a side line — like Hebridean crofters, while young Greenlanders were taken onto the farm at the Station and trained to take up farming as a full-time job.

It is among full-time sheep farmers that the striking successes are to be seen, and as all of these farms are built on the sites of medieval Viking homesteads, it is as though the very Norsemen had come back with their flocks and herds and taken up domestic life again.

This is an apt comparison for the best Greenlandic farms of the present-day remind one constantly of their Icelandic counterparts, and the latter have continued in unbroken line since the same Vikings founded them in the tenth century.

The best Greenlandic farm (but there are only half a dozen such) stands on its fenced homefield with stalls and sheepfolds nearby. The farmhouse is of wood and may have 4–8 rooms in two storeys. Inside, in the kitchen bread is baked and even butter and cheese made on occasion. The talk is of sheep: the number of lambs the flock has produced in the spring, for on this depends the number sold to the Royal Greenland Trading Company for slaughter in the autumn and their eventual cash income for the year, of round-ups, of hiring the Station's tractor and driver to clear new ground for hay, and of the low prices paid for their mutton. The farm dogs lie around the porch and the hens are scratching on the grass in front of the house. On the water of the fjord, a

couple of hundred yards away, is the motor boat that makes their connection with the trading store at the nearby settlement.

It is a dramatic change from the old seal hunting routine and it is rare to find a Greenlander who has gone straight, so to speak, from the kayak to the scythe. Sheep farming has taken the best of the young men and there is still room for more of them. Away from the coastline, inland, untenanted Viking sites are still waiting for the Greenlander who is brave enough to leave the outer coast with its seals and take to sheep.

Studies of the Grinnell Glacier, Baffin Island

During the summer of 1952 J. H. Mercer (leader) and W. Blake carried out glaciological and geomorphological studies in southeastern Baffin Island as part of the McGill University-Arctic Institute Carnegie Program. The party was flown to Frobisher Bay airbase by the R.C.A.F. in May. Unfortunately they were held up by ice conditions in the bay until mid-July and could not therefore obtain a complete record of the ablation period.

The main area investigated was the seven-by-twelve mile Grinnell Glacier and several nearby corrie glaciers. A thermograph and a rain gauge were set up on a 2,000-foot nunatak on the glacier, or small ice cap, which rises to 2,860 feet. On this small ice cap the yearly accumulation of snow does not all melt as on the Barnes Icecap to the north, and the ice cap is nourished both by the accumulation of firn at higher levels and by the formation of superimposed ice lower down. Several of the outlet tongues of the ice cap were visited, and from a comparison with photographs taken in 1897 it appears that although the ice cap is shrinking, it is doing so only slightly, and is in a fairly healthy state. A short trip was made to the nearby Terra Nivea ice cap, and on this journey one outlet tongue of the Grinnell Glacier was found to be advancing.

A large elevated delta and many raised beaches were examined in the area, as well as various moraines. The bedrock is mostly Archaean gneiss, often highly contorted, but there are some schists, quartzites, and granites. Geological, botanical, and entomological collections were made throughout the summer, and a large number of photographs were taken of the various glaciers and other landforms.

Many ducks, geese, gulls, and ptarmigan were seen, as well as ravens and snow buntings. Polar bears, seals, and beluga abounded, but arctic hares, foxes, and lemmings were not seen, although they are usually found in the area.

The weather was fine throughout most of the summer except for one week of sea fog brought in by southeast winds. It was only in May and August that freezing temperatures occasionally occurred.

The party returned to the airbase by ship at the end of August.

On July 13 of this year J. H. Mercer returned to the Grinnell Glacier to continue last summer's work. He will concentrate primarily on a study of the raised beaches and the various corries and outlet glaciers along the coast.

W. Blake

A new carbon drawing ink

A Tulsa, Oklahoma, firm has recently produced a carbon drawing ink for use on glass, cellulose acetate, and other water repellant surfaces which is not damaged by freezing and thawing. They therefore consider that it may have special value for use in the north, and have offered to provide up to 100 samples to those who are willing to test this ink under arctic conditions. Work done with the ink can be rendered water resistant by a brief cure at 180°F. The manufacturer's address is: Electrochemical Laboratories, 1430 Terrace Drive, Tulsa, Oklahoma, U.S.A.

OBITUARY

Richard Bögvad, 1897–1952

Richard Bøgvad, a Fellow of the Arctic Institute since December 1950, died suddenly from a heart attack on 7 August 1952 when on a mountain trip near Ivigtut in south Greenland.

Sidney Richard Emil Bøgvad was born in Frederiksberg, Copenhagen, on 21 November 1897. In 1924 he began his lifelong association with the Kryolitselskabet Øresund A/S (the Cryolite Company in Copenhagen, then called Øresunds chemiske Fabriker) in a clerical position. He was generously permitted to spend part of his time on studies at the University of Copenhagen, and received his degree in 1931. Even before his graduation he had been employed in research at the company's laboratory, and in 1929 he was sent to northeast Greenland to investigate a reported occurrence of cryolite. Various circumstances forced the expedition to winter in the Arctic, and Bøgvad took the opportunity to carry out geological field work in little-known areas of northeast Greenland.

After 1931 Bøgvad, who later became Chief Geologist at the Cryolite Company, spent practically every summer in southwest Greenland examining the cryolite at Ivigtut and searching for new deposits in the vicinity.

Bøgvad was one of the few Danish geologists who was connected with the mining industry, and it was therefore both natural and fortunate that he should take part in the founding of Grønlands geologiske Undersøgelse (Geological Survey of Greenland) in 1946. Later he became one of the geological advisers to the company which is now exploring the lead deposits at Mestersvig in east Greenland. The small mining industry on the Faroe Islands has also profited from Bøgvad's advice.

As well as being an able and conscientious economic geologist, Bøgvad was deeply interested in pure science. This led him to take part in Dr. Knud Rasmussen's Sixth and Seventh Thule expeditions to southeast Greenland, in the summers of 1932 and 1933, respectively. Bøgvad published a large number of articles on new minerals, most of them from the cryolite deposit, and on geological subjects of a more general character.

Richard Bøgvad will always be remembered for his upright character and for the high quality of his work.

J. C. Troelsen